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SAND DUNE TIGER BEETLES IN WESTERN CANADA: COMMUNITY ECOLOGY, COLOURATION, AND HISTORICAL BIOGEOGRAPHY.

by

JOHN HARRISON ACORN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

FALL, 1988

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ISBN 0-315-45555-1

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NAME OF AUTHOR: John Harrison Acorn

TITLE OF THESIS: Sand Dune Tiger Beetles in Western Canada: Community Ecology, Colouration, and Historical Biogeography.

DEGREE: Master of Science

YEAR THIS DEGREE GRANTED: 1988

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Date: Oct. 7, 1988

Chuang Tzu and Hui Tzu had strolled on to the bridge over the Hao, when the former observed, "See how the minnows are darting about! That is the pleasure of fishes."

"You not being a fish yourself," said Hui Tzu, "how can you possibly know what consists the pleasure of fishes?"

"And you not being I," retorted Chuang Tzu, "how can you know that I do not know?"

"If I, not being you, cannot know what you know," urged Hui Tzu, "it follows that you, not being a fish, cannot know in what consists the pleasure of fishes."

"Let us go back," said Chuang Tzu, "to your original question. You asked me how I knew in what consists the pleasure of fishes. Your very question shows that you knew I knew."

Chuang Tzu
c. 400 B.C.

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Sand Dune Tiger Beetles in Western Canada: Community Ecology, Colouration, and Historical Biogeography" submitted by John Harrison Acorn in partial fulfillment of the requirements for the degree of Master of Science in Entomology.

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ABSTRACT

Various aspects of the natural history of sand dune tiger beetles bear on the identification of which factors responsible for geographic colour variation among and within species. Pitfall trap data showed that five species of sand dune tiger beetles (*Cicindela* spp.) on the Empress dunes of Alberta and Saskatchewan are psammobiontic (strongly associated with sand). Two (*C. limbata* Say and *C. lepida* Dejean) live in open sand habitats, while the other three (*C. formosa* Say, *C. scutellaris* Say, and *C. lengi* W. Horn) live in more vegetated areas. These five species show two life history patterns: hibernation by larvae only or by both larvae and adults. In 1984, predation by newly emerged adult *C. formosa* appeared to cause declines in the abundances of both *C. limbata* and *C. lepida*, but this effect was not seen in1986, when phenologies of these three species were compared at Empress (where *C. formosa* is common) and Burstall (where it is rare).

Patterns of phenology, habitat use, and mandible length have been used as evidence that interspecific competition determines coexistence and relative abundance among sympatric tiger beetles. My results suggest otherwise, and I argue that species specific thermal requirements, and mimicry by *C. s. scutellaris* may be sufficient to explain the observed pattern of habitat use, and that phenological data do not show seasonal segregation of adults among species. Adult *Cicindela s. scutellaris* mimic the meloid beetle *Lytta nuttalli* Say. I argue that the colouration of many cicindelids may be mimetic, and that the tropical tiger beetle *Pseudoxycheila bipustulata ceratoma* Chaudoir mimics a mutillid wasp. Colouration also affects thermoregulation, and this effect was compared between subspecies with expanded and non expanded light elytral markings for both *Cicindela limbata* and *C. formosa*. Warming and cooling rates differed between subspecies for *C. limbata* but not *C. formosa*. Elytral markings did not affect seasonal or daily patterns of activity in *C. limbata*, but did affect thermoregulatory time budgets for both species. Beetles with non-expanded light markings maintained greater activity during cool periods, while those with expanded markings maintained greater activity during very warm periods. Body size and leg length may also affect thermoregulation. The geographic distributions of subspecies are hypothesized to be largely the result of Holocene changes in the extent of open sand habitats in the Great Plains. Large dune fields served as refugia for *Cicindela* during periods when small dunes were stabilized by plants. On large upland dune fields south of the boreal forest, a number of populations developed expanded light elytral markings. These distinctive light coloured populations were isolated in large dune fields during periods of cool climate, and expanded their ranges to intergrade with darker populations during periods of warm climate, or after human disturbance of sandy areas.

ACKNOWLEDGEMENTS

Although most of the people who have helped significantly in this study are acknowledged in the chapters to which their contributions apply, I have also received aid and encouragement throughout the production of this thesis by a few individuals who deserve prominent mention here. Dr. John Spence, my supervisor, has been an inspiration, a friend, and a patient source of direction for the past four years. Dr. George Ball acted as interim supervisor while Dr. Spence was on sabbatical leave, and I thank him for his contributions to my research, and for many long Saturday morning talks about tiger beetles, and entomology in general. For sheer volume of discussion, however, I am indebted to my friend Felix Sperling, who was always ready with a fresh pep talk, and a new way of approaching old problems. Lori Shortreed has been my closest friend throughout the thesis project, and probably knows as much as anyone the ups and downs that were involved. Her companionship and perceptive encouragement have been a big help along the way. I also owe thanks to my parents, Glen and June Acorn, who have encouraged and partly financed my research, and who have always supported my entomological pursuits.

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CHAPTER I

INTRODUCTION

Biologists study some insects because of their economic or medical importance, others because they represent easily manipulated systems for answering broad biological questions, and others because they are inherently interesting in themselves. The family Cicindelidae, the tiger beetles, has historically fallen in the latter category, and has attracted the attention of hundreds if not thousands of amateur and professional entomologists. Most diurnal species of tiger beetles are active, relatively large, strikingly coloured, difficult to catch, and interesting to watch. The family has a cosmopolitan distribution, and most temperate and tropical areas have enough of a fauna to stimulate the interest of local naturalists.

Behaviourally, diurnal adult tiger beetles in the genus *Cicindela* are adapted for thermoregulation in open-ground habitats where a complex visual system allows them to act as efficient predators (Dreisig, 1981; Gilbert, 1986; Kuster, 1979). Adult *Cicindela* increase their internal temperature by basking in direct sunlight, and reduce it by resting in the shade, holding the body high off the ground, taking short flights for convective cooling, and entering shallow burrows (Dreisig, 1980, Guppy, *et al.*, 1983, Morgan, 1985). Their thermoregulatory time budgets can be predicted by a general model, which applies to tiger beetles as well as diurnal lizards (Dreisig, 1985).

A number of studies have focussed on ecological interactions among species of tiger beetles, and between tiger beetles and other organisms. Studies of tiger beetle assemblages have provided evidence that interspecific competition among sympatric species has resulted in differences in phenologies, habitat associations, and structure (Pearson and Knisley, 1985; Pearson and Mury, 1979; Willis, 1967). The most important predators of adult tiger beetles appear to be birds, asilid flies, and lizards, which feed on large, intermediate, and small beetles respectively (Pearson, 1985). Larval *Cicindela* are parasitized by the larvae of some bombyliid flies and tiphiid wasps (Willis, 1967), and preyed upon by adult histerid beetles (Grandi, 1951, cited in Willis, 1967). One species of tiger beetle appears to show altruistic prudent predation, whereby adults increase the amount of food available to conspecific larvae by restricting their own predation (Wilson, 1978).

Tiger beetle colouration, the most immediately obvious attribute of these organisms, has also received attention from biologists. Shelford (1917) suggested that all tiger beetle elytral patterns were derived from combinations of 28 spots, but his unsupported assertion that the 28-spotted elytron represents the primitive, ancestral condition is not generally accepted. Many tiger beetles match their usual substrates in colour (Townsend, 1886) and tiger beetle colouration has been interpreted in terms of crypsis (Schultz, 1986; Willis, 1967), mimicry (Acorn, in press; Chapter III), thermoregulation (Chapter IV), intraspecific signalling (Pearson, 1988), and as aposematic warning colours (Pearson, 1985).

Tiger beetles have also been the subjects of historical biogeographic hypotheses, attempting to reconstruct primarily the post glacial events which have produced the geographic distributions apparent today (Freitag, 1965; Gaumer, 1977; Graves *et. al.*, in press; Rumpp, 1961; Spanton, in press; Wickham, 1904).

In Canada, interest in the Cicindelidae was stimulated greatly by the publications of Wallis (1961) and Freitag (1965). Freitag's work focussed on a problem of hybridization between two confusingly variable species, and similarly confusing variation in other species made Wallis' task of presenting a summary of the classification and distribution of the Canadian fauna very difficult indeed.

At the beginning of my research, it was apparent that the tiger beetles of sand dune habitats in western Canada could provide interesting material for study. Major dune fields in southern Alberta, Saskatchewan, and Manitoba have similar tiger beetle faunas at the species level, but not at the subspecies level. I approached the pronounced colouration differences among species and among subspecies within species, which have traditionally provided the source material for taxonomic studies, with the aim of elucidating the underlying causes of this diversity of colour patterns. After a general treatment of the habitat use and phenology of the dune tiger beetle assemblage in southern Alberta, I examined two potential functions of colouration; mimicry and thermoregulation. I then used this essentially ecological information as a basis for construction of an historical model to explain the present distributions of dune *Cicindela* species and subspecies.

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CHAPTER II

HABITAT ASSOCIATIONS, ADULT LIFE HISTORIES, AND SPECIES INTERACTIONS AMONG SAND DUNE TIGER BEETLES IN THE SOUTHERN CANADIAN PRAIRIES (COLEOPTERA: CICINDELIDAE)

INTRODUCTION

Although the study of tiger beetle ecology is in its infancy, most contemporary workers have argued that interspecific competition is important for determining relative abundance and coexistence of tiger beetle species. Food is a limiting resource in at least some tiger beetle communities, and this may result in competition for prey (Pearson and Knisley, 1985). This is consistent with the observation that mandible length of adult *Cicindela* is correlated with median prey size, and that the composition of tiger beetle assemblages may be determined by the size range of available prey (Pearson and Mury, 1979). Adults of some tiger beetles in saline habitats show different habitat associations and phenologies thus avoiding one another in time and space, although there is much overlap among species with respect to both of these measures (Willis, 1967). Thus, tiger beetle assemblages have shown patterns of resource partitioning with respect to time, space, and food, all of which appear to be the result of competition.

Predation also affects tiger beetle populations, and possibly the composition of tiger beetle assemblages. The most important predators of adult tiger beetles are birds, asilid flies, and lizards, which feed on large, intermediate, and small beetles respectively (Pearson, 1985). Larval *Cicindela* are parasitized by the larvae of some bombyliid flies and tiphiid wasps (Willis, 1967), and preyed upon by adult histerid beetles (Grandi, 1951, cited in Willis, 1967). It has been argued that differences in thermoregulatory behaviour might modify diel activity patterns to ameliorate the effects of predation and competition for adults of some *Cicindela* species (Pearson and Lederhouse, 1987).

In this paper, I deal with the following questions about sand dune tiger beetles (genus *Cicindela*) in southern Alberta and Saskatchewan: 1) is there a particular assemblage of species associated with open dune habitats; 2) how do adults compare with respect to habitat associations and phenology; and 3) are patterns elucidated by the latter comparisons best interpreted in terms of interspecific competition, responses to predation, or other as yet unidentified factors?

METHODS

The Empress Dune field Study Site

Field work was carried out on the Empress dune field, approximately 11 km south of Empress, Alberta, on a point bar in a bend of the South Saskatchewan River, straddling the Alberta-Saskatchewan border (Plate II-1). Here, Tertiary and Quaternary sands, gravels, silts and clays have been reworked and sorted by the river and prevailing winds, resulting in numerous sand dunes, although only a few areas of open, blowing sand exist today. The surrounding mixed prairie is mainly used for grazing, and is broken by extensive cropland. The river valley is forested primarily by *Populus*, *Acer*, and *Prunus*. The Empress dunes are one of a number of large dune fields in southern Alberta and Saskatchewan.

Five areas of the Empress dune field were chosen for intensive sampling, and given names (Fig. II-1). These areas were chosen to represent dunes in various stages of being stabilized by plants. River Dune and Big Dune are two of the three actively moving dunes in the dune field. They differ in topography in that River Dune is on the eastern edge of the dune field, and extends from an area of stabilized dunes (covered mainly by grasses, with *Rosa woodsii* Lindl., and *Prunus virginiana* L. in sheltered areas) down the river valley into riverine forest, while Big Dune is near the middle of the dune field, among more stabilized dunes. Personal observations of Home Dune over the last 15 years suggest that the dune is now undergoing rapid stabilization (primarily by *Psoralea lanceolata* Pursh) since the crest has been colonized by *Calamovilfa longifolia* (Hook.) Scribn., even though there is still much open sand on this dune. Stable Dune has been completely covered by vegetation (primarily grasses, *Rosa* and *Prunus*) since I first visited the site in 1973, except for a very small (c. three m^2)

bare area near the dune's crest, but aerial photographs reveal it was an open, blowing sand dune as recently as 1962. The area between Grassy Dune and Big Dune is vegetated primarily by *Stipa comata* Trin. and Rupr. and *Koeleria macrantha* (Ledeb.) J. A. Schultes f., while Grassy Dune itself is covered in part by *Rosa*. This dune possesses a discernable organic A horizon in the sandy soil, which the other dunes do not have.

In the terminology of Hulett *et. al.* (1966) Big Dune, River Dune, and Home Dune are "active complexes," a physiographic category characterized by ongoing erosion and deposition. Stable Dune is a "stabilized dune," since it show no evidence of recent erosion. The Grassy Dune transect passes from a "sand flat" area to another "stabilized dune." Essentially, the categories arrived at by these workers reflect the same axis of increasing stabilization of once open sand which served as the subjective basis for my own choice of areas on which to place the transects.

Other Study Sites

Additional observations and collections were made at a sandy blowout near Nestow, Alberta, and at dunes 5 km north of Burstall, Saskatchewan, and 25 km east of Fox Valley, Saskatchewan. Open sand at Nestow was caused by railroad construction in Quaternary sands, and is surrounded by forests of *Populus tremuloides* Michx., *Pinus banksiana* Lamb., and *Picea mariana* (Mill.) BSP.. The two active dune fields in Saskatchewan share the same geological origin as the Empress dune field, and are presumably of natural origin, unassisted by human disturbance. The floras of these and the Empress dunes are typical of prairie dunes in western Canada. The Fox Valley dunes are part of the Great Sand Hills of Saskatchewan.

Pitfall Trapping

White plastic pitfall traps (diameter: 11 cm, depth: 13 cm, filled to a depth of approximately 5 cm with automobile antifreeze [primarily ethylene glycol]) were used to collect adults of *Cicindela* on the Empress dunes. Traps were placed in five transects, oriented parallel to the direction of dune movement and prevailing winds, since this is the axis along which most visible variation in topography and vegetation is evident. Although the dunes sampled were of different sizes, 50 m transects, each with ten traps spaced 5 m apart, allowed coverage of at least the windward face of each dune (Fig. II-1). The transects were placed on the five dunes described above.

Traps were buried with their top edge flush with the ground, without covers, and were harvested once a week. Rainfall was infrequent and any accumulated rainfall in the traps evaporated quickly during warm weather. Drifting sand posed the greatest problem, either filling or drifting away from traps, so that traps in open sand locations rarely remained functional for the entire week. Traps which frequently filled with sand were provided with extra antifreeze, and as long as some antifreeze remained into which specimens could fall, the traps worked. Sand from filled traps was sieved through a kitchen strainer with approximately 2 mm mesh, and many such traps contained large numbers of beetles, preserved in the sand and antifreeze mixture.

Pitfall traps were monitored from June 2 to August 27, 1984, during the main period of adult tiger beetle activity, which was observed to extend from early April through early October.

Strictly speaking, the number of beetles caught in pitfall traps can be interpreted only in terms of beetle activity in the area sampled (Southwood, 1978). Activity of adult *Cicindela* consists largely of thermoregulatory behaviour, which is affected by temperature and solar radiation (Dreisig, 1980, 1981, 1985; Pearson and Lederhouse, 1987). Upper and lower temperature thresholds for activity show little variation among species (Pearson and Lederhouse, 1987), and adult *Cicindela* apparently do not show seasonal shifts in habitat use (Pearson and Mury, 1979; Willis, 1967). Thus, weather may account for some variance in trap collection data, but I assume that these effects are of comparable magnitude for all species, and that comparisons among species are thus valid. The object of this work was to determine which areas of the dune constitute the habitat for adults of each tiger beetle species. The term habitat, as I use it here, follows the usage suggested by Southwood (1987), meaning " the area of the environment that provides the resource requirements for a discrete phase of its life."

To determine whether aspects of the vegetation were associated with tiger beetle distribution within the dune environment, percent canopy cover, and the species of plants present in the area around each trap (one m^2) were recorded, since tiger beetles are characteristically associated with particular soils, and amounts of canopy cover (see Wallis [1961] for qualitative descriptions of the habitats of Canadian species). Photographs of all traps, taken June 4, 1984, were scored for percent canopy cover around the traps, using an Apple II Plus microcomputer with a digitizing tablet. Traps were assessed for similarity to one another using Jaccard's coefficient of similarity, based on presence or absence of plant species (listed in Appendix I-1), and then again using tiger beetle species. Values for Jaccard's coefficient were clustered using an average distance algorithm to give a means of summarizing the plant and beetle data gathered at the trap sites. Janson and Vegelius (1981), in comparing various ecological similarity coefficients, recommend Jaccard's coefficient as an excellent measure of ecological association. My purpose here was to allow comparison of trap sites with respect to the organisms present at them, so that these comparisons could be used as predictors of tiger beetle distributions among the areas sampled. I have also attempted to relate the groupings I arrived at to the physiographic categories established by Hulett *et. al.* (1966) for vegetaton on dune sands in the grasslands of Saskatchewan.

Frequencies of beetle captures were compared with respect to all four trap grouping arrangements (by transects, by canopy cover, by clustering based on plants and by clustering based on beetles), using *G*-tests. All numerical calculations were performed on the mainframe Amdahl 5870 computer at the University of Alberta using the Midas statistical program (Fox and Guire, 1976), except *G*-tests, which were performed on a hand calculator.

Measurements

Mandible length was measured with an ocular micrometer in a Wild M5 dissecting microscope, for right mandibles dissected from adult specimens. Length was measured dorsally, in a straight line, from the tip of the mandible to the center of the dorsal articulation, as described by Pearson and Mury (1979).

Studies of Predation

Observations of predation by *C. formosa* (both *C. formosa formosa* and *C. formosa gibsoni* Brown) were made in August 1986. Wild beetles (at the Empress and Fox Valley dunes) as well as 14 individuals with cyanoacrylate glue on their wings, which prevented them from flying, were observed, and the numbers and identities of their prey were recorded. These latter beetles were observed for a total of 9.5 hours: two hours on the Empress dunes; two hours on the Burstall dunes; and 5.5 hours at Nestow Alberta, outside the natural range of *C. formosa*, but in an area occupied by *C. limbata*.

The phenology of *C. limbata* Say, and *C. lepida* Dejean were compared at Empress (in the presence of large numbers of *C. formosa* Say) and Burstall (where *C. formosa* is extremely uncommon), as a natural experiment. The dune fields, which are 18 km apart, share nearly identical floras, faunas, and sand composition, although the Burstall dunes may have a somewhat higher water table. Every week, from July 21 to Aug 21, 1986, I walked a set route at both dune fields, identifying by sight all beetles within 2 m of my path. At Empress I walked around the periphery and through the center of River Dune, and a similar route was taken on a similar size dune at Burstall. Observations were made in mid to late morning, and only under sunny conditions.

RESULTS

Pitfall Trapping and Habitat Associations

In total, 4443 tiger beetles were collected in the pitfall traps (2027 *C. formosa*, 1246 *C. limbata*, 606 *C. lepida*, 298 *C. scutellaris* Say, 250 *C. lengi* W. Horn, 11 *Cicindela punctulata* Olivier, 7 *C. tranquebarica* Herbst, and 5 *Cicindela nebraskana* Casey). Because of small sample size, the latter three species are not included in most analyses below.

For all measures (traps grouped by transects, degree of canopy cover, cluster analysis based on plant species, and cluster analysis based on tiger beetle species), frequencies of capture for all five common tiger beetle species showed significant differences (based on *G*-tests) from the null hypothesis that all traps would be equally likely to capture beetles (Table II-1, II-2, II-3, and II-4). All four measures were not, however, equally useful in elucidating habitat associations of the beetles.

With respect to transects, all species except *C. lengi* were more frequently caught on the Big Dune than elsewhere (Table II-1), suggesting that larger dunes may support proportionately larger tiger beetle populations. The Big Dune transect yielded the most specimens overall, followed by the River Dune and Home Dune transects, while few specimens were collected from the Stable Dune and Grassy Dune transects. This corresponds with decreasing order of open sand area on the respective dunes, and shows clearly an association of dune tiger betles with active complexes (*sensu* Hulett *et. al.*, 1966). However, numerous traps on different dunes were similar with respect to canopy cover and flora, suggesting that the beetles might discriminate between habitats at a finer scale than among entire dunes.

When traps were grouped by percent canopy cover an unexpected pattern emerged, with all beetle species frequent in areas of very high percent cover whereas areas with low percent cover were not associated with particularly high tiger beetle numbers (Table II-2). This pattern exposed a weakness in this method, since it grouped trap sites in grassy areas (with no open sand at ground level, but dense growth of *Koeleria* and *Stipa* grasses)) with dune margin traps in dense *Psoralea* growth (with much open sand beneath a canopy of leaves). Had vegetation cover been measured at ground level rather than from above, a more meaningful analysis would likely have resulted.

It was, however, possible to distinguish between dune margin areas and grassy areas when traps were grouped by cluster analysis of plant species present at each trap site. The traps were classified into four groups based on the cluster analysis (Fig. II-2): 1) open sand, 2) scurf pea, 3) stabilized dune, and 4) sand flat. The open sand group comprised trap sites in actively moving sand with little or no vegetation, on the windward and slip faces of active dunes. The scurf pea group comprised trap sites from the windward faces of dunes in the process of stabilization, and on the very edges of active dunes, vegetated primarily by *Psoralea*, with some actively moving sand. The stabilized dune group comprised trap sites primarily vegetated by *P. lanceolata*, but much more densely, and with no trace of actively moving sand. Other plant taxa at these sites include *Koeleria macrantha*, and *Calamovilfa longifolia*. The sand flat group comprised trap sites with vegetation composed primarily of *Artemisia frigida* Willd., *Calamovilfa longifolia*, *Koeleria macrantha*, and *Stipa comata*. Traps in scurf pea group yielded the most beetles, followed by open sand, stabilized dune, and sand flat groups respectively (Table II-3). All ten of the Big Dune traps were in the scurf pea group, and this provides a more likely explanation for the high predominance of tiger beetles.

Habitat use, based on cluster analysis of plant species, differs among tiger beetle species (Table II-3). *Cicindela lepida* and *C. limbata* were strongly associated with open sand and scurf pea trap groups. *Cicindela formosa* shows a strong though not exclusive association with the scurf pea group. *Cicindela scutellaris* and *C. lengi* are both strongly associated with bare sandy habitats throughout their geographic ranges, and on the Empress dunes they seem most common in dune margin and pioneer vegetation areas. Some rare species were too uncommon to allow meaningful analyses of habitat use (*C. tranquebarica*, *C. punctulata*, *C. nebraskana*, *C. purpurea* Olivier and *C. decemnotata* Say [one specimen each of the latter two species, collected by hand]), but of these only *C. tranquebarica* and *C. decemnotata* were collected in open sand and scurf pea traps. Thus, there is a psammobiontic (associated with sand) *Cicindela* assemblage at Empress which consists of five abundant species, two of which are associated primarily with open sand and scurf pea areas, three of which are associated with scurf pea and stabilized dune areas. Although five other rare species were encountered on the dunes, they generally occur in other habitats and should not be considered psammobiontic.

Two biases are likely in the data presented in Table II-3. First, the open sand traps were probably undersampled because of traps filling with sand. Second, the first few traps on the Grassy Dune transect, adjacent to the slipface of the Big Dune, consistently captured species typical of open sand areas rather than the stabilized sand flat area immediately surrounding the traps. This was likely caused by dune insects being blown off the Big Dune into the sand flat area, a phenomenon which I observed numerous times.

Clustering of trap sites on the basis of beetle species present produced four identifiable groupings of trap sites (Figure II-3). It is possible to identify areas of open sand, dune margin areas dominated by sparse growth of *Psoralea*, heavily vegetated areas on stable dunes and sand flats, and heavily vegetated areas lying in low spots between stable dunes. This pattern is in basic agreement with the groupings identified using plant species, corroborating the usefulness of the latter method.

Some traps clustered differently in the two analyses. Traps RD5 and BD10 were in the open sand group in one analysis and the scurf pea group in the other. Both traps were on the margin of patches of *Psoralea* growth, and thus represent intermediate areas. Numerous traps were in the scurf pea group in one analysis and a more heavily vegetated group (stabilized dune or sand flat in Fig. II-2; heavily vegetated or vegetated low areas in Fig. II-3) in the other. Of these, HD1, HD2, HD3, HD4, and HD9 were all on a small dune very close to stabilization, while SD4 may have attracted beetles because the cleared area around the trap represented a very small opening in a grassy area. Both BD1 and RD1 were situated well into the stabilizing trailing end of their respective dunes, and thus were perhaps beginning to show characteristics of newly stabilized areas.

Life Histories

Data from pitfall traps show two life history patterns. In one, adults emerge in late summer, overwinter in burrows, and reappear the following spring; best shown by *C. scutellaris* (Fig. II-4). The histogram is distinctly bimodal, with the first newly emerged adults appearing about August 2, and adults which overwintered the previous winter surviving until July 19. *Cicindela lengi*, *C. formosa*, and *C. limbata* (Figs. II-5 to II-7) are more difficult to interpret, but all three overwinter as adults. Adults of these species may survive later into the summer, and show increased activity (thus likelihood of being caught by pitfall traps) during warmer weather in mid summer, resulting in data which are difficult to interpret. *Cicindela limbata* emerged from pupation the week after I quit monitoring the traps, thus emergence of teneral adults is not indicated on Figure II-7. The second life history pattern is seen in *C. lepida*, which emerged from pupation in early July, and disappeared before the onset of fall (Fig. II-9). No attempt was made in this study to determine the length of the life cycles of these species.

Mandible Length

C. *lepida* and *C. limbata* from the Empress dunes showed considerable overlap in mandible length (*C. lepida* : 2.47± 0.082 mm, *C. limbata* : 2.42± 0.109 mm, [t= 1.64 , p>0.1, n=20 for both species]), with a difference ratio of 1.02. The other psammobiontic species at Empress showed comparable mandible lengths to those reported from Fox Valley (Pearson and Mury,1979) (*C. scutellaris* : 3.29±0.095 mm, *C. lengi* : 3.42±0.104 mm, *C. formosa* : 4.10±0.148 mm).

Predation

Predation on adult *Cicindela*, except by *C. formosa*, was not observed in this study. Birds and asilid flies are common on the dune field, but lizards are not present. Potential predators and parasites of larvae observed on the dunes included bombyliid flies, the tiphiid wasp *Methocha* (probably *M. stygia* Say, but possibly *M. californica* Westw.), and histerid beetles.

I observed adult *C. formosa* feeding on adult *C. limbata* three times; once in August, 1984, and twice in August, 1985. *Cicindela formosa* is an impressive predator; on Aug 14, 1985 I observed an adult *C. formosa gibsoni* attack and kill an adult sphecid wasp (*Bembix* sp.) approximately as large as the beetle itself. However, of eight observations of predation by *C. formosa* in August of 1986, none involved other *Cicindela* adults, although nine out of 13 unsuccessful attacks on other insects were on adult *C. limbata nympha*. Other insects eaten were ants (four), acridid grasshoppers (one), lepidopteran larva (one), and the ladybird beetle *Coccinella transversoguttata richardsoni* Brown (two).

Phenology data are consistent with the proposition that *C. formosa* may prey on *C. lepida* and *C. limbata*. The mean number of beetles per trap declined markedly for *C. lepida* and *C. limbata* at about the time that *C. formosa* adults emerged from pupation. No such interaction is apparent between *C. formosa* and *C. lengi* or *C. scutellaris*, possibly since the adults of the latter two species are large enough to avoid falling prey to the very large adults of *C. formosa*.

However, in 1986 the Empress populations of *C. limbata* and *C. lepida* did not decline with the emergence of *C. formosa*, and showed no appreciable phenological differences from populations at Burstall where *C. formosa* is uncommon (Fig. II-9). Both populations of *C. limbata* seemed to increase in abundance in mid August, but since no newly emerged *C. limbata* were found this probably reflects differences in activity during the data gathering periods rather than changes in abundance. Day to day observations in 1984 and 1986 suggest that *C. limbata* was in fact very rare after the first week of August, 1984 at the Empress dunes, and that this did not occur in August of 1986.

In general, the summers of 1984 and 1985 were warmer and drier than that of 1986. High temperature and lack of moisture, rather than predation by *C. formosa*, may be responsible for the decline in *C. limbata* populations seen in 1984. Or, temperature and humidity may affect the extent to which *C. formosa* feeds on smaller *Cicindela* adults, possibly acting on the abundance of other prey organisms..

For *C. formosa* and *C. scutellaris*, far more newly emerged adults were trapped than adults which had overwintered the previous year, possibly indicating high overwintering mortality.

This was not true for *C. limbata* or *C. lengi*.

DISCUSSION

Dune Habitat Associations of Tiger Beetles

The five most common species of *Cicindela* on the dunes (*C. limbata, C. formosa, C. scutellaris, C. lengi,* and *C. lepida*) are all strongly psammobiontic. These species are associated with sandy areas throughout their geographic ranges (Gaumer, 1977; Wallis, 1961), and in New Mexico, *C. formosa, C. scutellaris, C. lengi* and *C. lepida* show highly restricted habitat associations on sand flats and dunes, and higher population densities than *Cicindela* in other habitats (Knisley, 1984).

Of the non-psammobiontic species, *C. tranquebarica* was found on open sand on the Empress dunes, but is also associated with clay, mud, and gravelly soils in other areas (Wallis, 1961). *Cicindela nebraskana* and *C. punctulata* were associated with stabilized dune and stabilized sand flat habitats on the Empress dune field, in agreement with their habitat associations in other areas (Spanton, in press; Wallis, 1961). *Cicindela purpurea* and *C. decemnotata* adults are present only in the early spring and late fall and neither species is associated with open sand or dune margin habitats (Wallis, 1961).

Although the other four psammobiontic species are known from all major dune fields in southern Canada, *C. formosa* is absent from numerous dune areas in the Canadian prairies (Wallis, 1961), such as the Burstall, Saskatchewan dunes, and the Great Sand Hills of Saskatchewan south of Sceptre. It is possible that *C. formosa* requires deep, well drained sand (Gaumer, 1977), and the Saskatchewan dune areas mentioned support the growth of *Salix* and *Populus*, indicating more mesic soils than are present at Empress.

Life Histories and Predation Among *Cicindela* Adults

Tiger beetle show two general types of life histories. In one, both adults and larvae hibernate, in the other adults are present only in mid summer and only larvae hibernate (Criddle, 1907). Shelford (1908) identified three life history types, two of which involved hibernation by larvae only, but differed in the number of winters (one or two) spent as a larva. In Manitoba, some species which hibernate as both adults and larvae have a three year life cycle (Criddle, 1910) while the same species in the Chicago area have a two year life cycle. Thus, the two basic life history patterns can each be subdivided to give four general types (and perhaps more if one or four year life cycles are possible). Of the psammobiontic species at Empress, only *C. lepida* hibernates as larvae only, while *C. formosa*, *C. limbata*, *C. lengi*, and *C. scutellaris* hibernate as both adults and larvae. The length of life cycles at Empress is still unknown, but in Manitoba, at comparable latitudes, *C. formosa*, *C. limbata*, and *C. lengi* all have three year life cycles, while *C. lepida* has a two year life cycle (Criddle, 1910).

C. limbata emerged almost a month later than *C. formosa* and *C. scutellaris* on the Empress dunes. Late emergence in *C. limbata* may reduce predation by *C. formosa* on pre-reproductive *C. limbata*, but the significance of this as a selective force shaping phenology remains to be established.

The suggestion that *C. scutellaris* and *C. formosa* are subject to higher overwintering mortality than *C. limbata* and *C. lengi* may explain differences in the geographic ranges of these species. The former two species are near the northern limit of their geographic ranges, while the latter are found well into the boreal forest to the north (Wallis, 1961).

Interspecific predation occurs among the *Cicindela* of the Empress dunes, and deserves further study since its significance has not been established. Observations of predation by *C. formosa* on *C. limbata*, decline in abundance of the latter species and *C. lepida* in the presence of newly emerged *C. formosa* in 1984, and the fall emergence of *C. limbata* and summer emergence of *C. lepida* all provide evidence for the importance of this interaction.

In agreement with my observations in 1984, but not 1986, Criddle (1907) observed in Manitoba that "towards the end of July, a great many [*C. limbata*] die off," although he did not attribute this to predation by *C. formosa*. An alternative explanation for the decrease in numbers of *C. limbata* and *C. lepida* in 1984 at Empress could be that the beetles activity, rather than abundance, decreased. This is unlikely, since migration to other habitats has not been reported for adult *Cicindela*, and cessation of activity would give these beetles, which are very near the end of their lives, no future opportunity to reproduce in the absence of *C. formosa*.

Although tiger beetles are readily cannibalistic in captivity and when confined in collecting bottles, *C. formosa* is the only member of its genus reported to feed upon other adult *Cicindela* in the field. In Peru, Pearson and Anderson (1985) observed large *Megacephala* (nocturnal tiger beetles) feeding on small diurnal tiger beetles which had been removed from their nocturnal roosts in vegetation, but predation here was clearly the result of disturbance by the investigators.

Phenology, Habitat Use, and Competition

As many authors have recently argued, differences among species with respect to resource use in time and space are not necessarily the result of competition (eg. Schoener, 1982; Strong *et. al*., 1985). Whereas competition may promote differences in resource use among competing species, similar differences can also arise among sympatric species for other reasons. It is thus difficult to detect interspecific interactions even in sympatric assemblages of tiger beetles, where strong competition effects seems likely to develop among general predators in a harsh environment with presumably little food (Pearson and Knisley, 1985).

Pearson and Mury (1979) used data from the tiger beetle fauna of the Great Sand Hills of Saskatchewan to support the hypothesis that interspecific competition has resulted in character divergence with respect to mandible size in tiger beetle assemblages in areas with a wide range of prey sizes. They showed that *C. formosa gibsoni*, *C. scutellaris*, *C. lengi*, and *C. limbata* differed with respect to mandible length by an average ratio of 1:1.24. Unfortunately, one of the most abundant species in this assemblage, *C. lepida*, was omitted from Pearson and Mury's analysis, probably because *Cicindela lepida* is present only during July and early August, and would be missed by collectors at any other time of year. However, the activity period of *C. lepida* overlaps with those of the four other abundant species, such that if interspecific competition was taking place *C. lepida* would be expected to contribute substantially to it.

Adult *C. limbata* and *C. lepida* do not show character divergence with respect to mandible length. They occur in the same habitats (Tables II-1, II-2, and II-3) and, based on mandible length, are likely to feed on the same prey items. It is possible that these species minimize competition in ways other than prey choice. Adult *C. lepida* remain active nocturnally as well as diurnally on warm nights, and this may facilitate coexistence with diurnal *C. limbata*. *C. lepida* has secondarily evolved eyes of the scotopic A type, which are adapted for low light conditions, while *C. limbata* possesses photopic eyes, typical of most adult *Cicindela* and adapted for diurnal vision (Kuster, 1979). However, Vaurie (1950) collected *C. limbata* at lights at night, indicating that this species is also capable of nocturnal activity. Phenologically, the activity period of *C. lepida* is completely overlapped by that of adult *C. limbata*. It is unclear whether the magnitude of differences in diel and seasonal activity between these two tiger beetles is sufficient to reduce competition, or to serve as evidence of past competition. However, it is certain that Pearson and Mury's simple character displacement hypothesis is not corroborated by the mandible length of *C. lepida*.

Hilchie (1985) has suggested a complex scenario of interspecific interactions among *Cicindela* adults on the Empress dunes, based on casual observations of this assemblage, and emphasizing the role of competition. His scenario involves both seasonal and habitat segregation among species, which prevent interspecific competition, and predation by adult *C. formosa*, *C. scutellaris*, and *C. lengi* on adult *C. limbata* and *C. lepida*. He states that adult *C. lengi*, *C. lepida*, and *C. scutellaris* live in dune margin and grassland habitats, while *C. limbata* live in dune margins and open sand, except in the presence of other tiger beetles, when they moves away from dune margins.

Hilchie's (1985) scenario is inconsistent with many of my findings. I found no evidence that adult *C. scutellaris* and *C. lengi* feed on other tiger beetles. I found that adult *C. limbata* and *C. lepida* were both associated with open sand habitats, and that *C. limbata* is common throughout the period when adult *C. lepida* are active on the dunes, and therefore conclude that these species do not show seasonal segregation. I found no evidence that adult *C.*

limbata migrate away from dune margins in the presence of other tiger beetles, in fact *C. limbata* consistently shared the dune margin habitat with other tiger beetles.

The observed pattern of habitat use among the dune *Cicindela* at Empress can be reasonably explained without reference to competition and resource partitioning. I argue (Chapter III) that *C. scutellaris* mimics the meloid beetle *Lytta nuttalli* Say, which feeds on *Psoralea lanceolata* . The habitat of *C. scutellaris* corresponds to that of *L. nuttalli* and its foodplant; an expected consequence of mimicry. The small, light-coloured adults of *C. limbata* and *C. lepida* are more strongly associated with open sand habitats (which are warmer owing to lack of shade) than are the large, dark adults of *C. formosa* and *C. lengi*. This is consistent with the argument that lighter-coloured elytra allow tiger beetles to reduce heat loads in open, dry environments (Chapter IV). This explanation for the habitat associations of the Empress tiger beetles is based on the properties of individuals, rather than emergent properties of the species assemblage, and satisfies the criteria for reduction of explanation at the level of community ecology to explanation at the level of individual ecology (Schoener, 1986). Dune tiger beetles are indeed specialists in a thermally extreme habitat, and this fact should always be considered in interpretations of their ecological characteristics.

Thermoregulatory adaptations can easily be mistaken for the effects of competition and predation. In Arizona, *C. marutha* Dow and *C. fulgoris* Casey show diel segregation, which has been interpreted as the result of selection to avoid predators on the part of adult *C. marutha*, and to avoid adult *C. marutha* on the part of adult *C. fulgoris* (Pearson and Lederhouse, 1987). However, from the data presented, it is apparent that birds, lizards, and *C. marutha* adults are all most active from 1000-1100 and 1500-1600 h., and that these beetles do not in fact avoid the predators. Since *C. fulgoris* has expanded white maculations while *C. marutha* does not, the observed pattern is more parsimoniously interpreted as overheating during mid day for *C. marutha* (many adult tiger beetles cannot tolerate mid-day heat [Dreisg, 1980; Guppy et al., 1983; Wallis, 1961]) but not *C. fulgoris* (the activity pattern of *C. fulgoris* follows the daily curve for temperature, showing no evidence that the beetles reach an upper threshold for activity). Pearson and Lederhouse's data show that adults of these species do not differ with respect to upper temperature tolerance.

Pearson and Lederhouse also suggest that by staggering diel activity these beetles reduce predation on both populations, but contrastingly suggest for another assemblage of tiger beetles that high densities and synchronized activity also reduce predation. These arguments are inconsistent, and unnecessarily implicate predation and competition to explain a thermoregulatory adaptation of one species alone.

The foregoing is essentially an argument for consideration of factors other than intraspecific competition in interpretations of the community ecology of tiger beetles. I am not arguing that intraspecific competition does not occur, or that my data disprove its existence or importance in this assemblage. However, it is neither essential nor self evident for the construction of a consistent explanation for the patterns I have observed in the *Cicindela* of the Empress dunes.

ACKNOWLEDGEMENTS

I am grateful for many productive discussions with the following people: R. S. Anderson, J. L. and B. F. Carr, G. J. Hilchie, J.-F. Landry, D. R. Maddison, G. Ogilvie, F. A. H. Sperling, and D. A. Wrubleski. L. Shortreed provided assistance in the field. J. R. Spence gave me consistently excellent advice and encouragement. G. E. Ball critically reviewed the manuscript and made numerous helpful suggestions. A. W. Bailey provided advice and guidance with respect to matters related to plant ecology. A. Hardy suggested the design for sand dune pitfall traps. J. M. Cumming identified the tiphiid wasps. The Fowlie family was especially helpful, allowing me to work and camp on their land, and feeding me numerous hearty meals. Research costs were covered by grants from the National Science and Engineering Research Council of Canada to J.R. Spence.

II-1

	No. of samples	*Cicindela limbata*	*C. scutellaris*	*C. formosa*	*C. lengi*	*C. lepida*	All Species
Transects:							
River Dune	121	247 (2.04)	48 (0.40)	360 (2.98)	15 (0.12)	245 (2.02)	915 (7.56)
Big Dune	129	776 (6.02)	97 (0.75)	1008 (7.81)	66 (0.51)	305 (2.36)	2252 (17.5)
Home Dune	129	223 (1.73)	52 (0.40)	582 (4.51)	111 (0.86)	55 (0.43)	1023 (7.93)
Stable Dune	130	0 (0.00)	51 (0.39)	39 (0.30)	50 (0.38)	0 (0.00)	140 (1.08)
Grassy Dune	130	0 (0.00)	50 (0.38)	38 (0.29)	8 (0.06)	1 (0.01)	97 (0.75)
G- statistics	-	1709.0**	26.1**	1809.1**	148.3**	811.3**	3614.9**

II-2

	No. of samples	*Cicindela limbata*	*C. scutellaris*	*C. formosa*	*C. lengi*	*C. lepida*	All Species
Ground Cover:							
0-20%	225	379 (1.68)	63 (0.28)	382 (1.70)	62 (0.28)	247 (1.10)	1133 (5.04)
21-40%	90	91 (1.01)	60 (0.67)	516 (5.73)	47 (0.52)	53 (0.59)	767 (8.52)
41-60%	39	170 (4.36)	13 (0.33)	160 (4.10)	13 (0.33)	92 (2.36)	448 (11.5)
61-80%	26	0 (0.00)	9 (0.35)	36 (1.38)	9 (0.35)	0 (0.00)	54 (2.08)
81-100%	259	606 (2.34)	153 (0.59)	933 (3.60)	119 (0.46)	214 (0.83)	2025 (7.82)
G- statistics	-	264.0**	36.9**	393.2**	15.6*	130.5**	407.4**

Tables II-1 and II-2. Habitat associations of the Empress dune tiger beetles. For each species, figures show # of beetles collected in each category (means per trap per week in parentheses). For G- statistics, testing for differences from random distribution among categories, ** indicates $p < 0.001$, * indicates $p < 0.005$.

		No. of samples	*Cicindela limbata*	*C. scutellaris*	*C. formosa*	*C. lengi*	*C. lepida*	All Species
II-3	**Plant Associations:**							
	Open Sand	72	199 (2.76)	0 (0.00)	46 (0.64)	1 (0.01)	183 (2.54)	429 (5.96)
	Scurf Pea	295	938 (3.18)	176 (0.60)	1759 (5.96)	181 (0.61)	394 (1.34)	3448 (11.4)
	Stabilized Dune	182	109 (0.60)	106 (0.58)	216 (1.19)	67 (0.37)	29 (0.16)	527 (2.90)
	Sand Flat	90	0 (0.00)	16 (0.18)	6 (0.07)	1 (0.01)	0 (0.00)	23 (0.26)
	G- statistics	-	798.8**	103.0**	1601.8**	140.9**	527.2**	2406.0**
II-4	**Tiger Beetle Associations:**							
	Open Sand	72	280 (3.89)	0 (0.00)	27 (0.38)	0 (0.00)	122 (1.69)	429 (5.96)
	Scurf Pea	242	966 (3.99)	157 (0.65)	1683 (6.95)	155 (0.64)	482 (1.99)	3443 (14.2)
	Vegetated	260	0 (0.00)	138 (0.53)	317 (1.22)	79 (0.30)	2 (0.01)	536 (2.06)
	Vegetated Low Areas	65	0 (0.00)	3 (0.05)	0 (0.00)	16 (0.25)	0(0.00)	19 (0.29)
	G- statistics:	-	1770.7**	125.5**	1920.7**	98.0**	837.7**	3406.0**

Tables II-3 and II-4. Habitat associations of the Empress dune tiger beetles. For each species, figures show # of beetles collected in each clustering category (means per trap per week in parentheses). For G- statistics, testing for differences from random distribution among categories, ** indicates $p < 0.001$, * indicates $p < 0.005$.

Plate II-1. Air photograph of the Empress dune field, taken on 2 May, 1982, showing the locations of pitfall trap transects (scale= 1:60,000). Abbreviations stand for Big Dune (bd), River Dune (rd), Home Dune (hd), Stable Dune (sd) and Grassy Dune (gd).

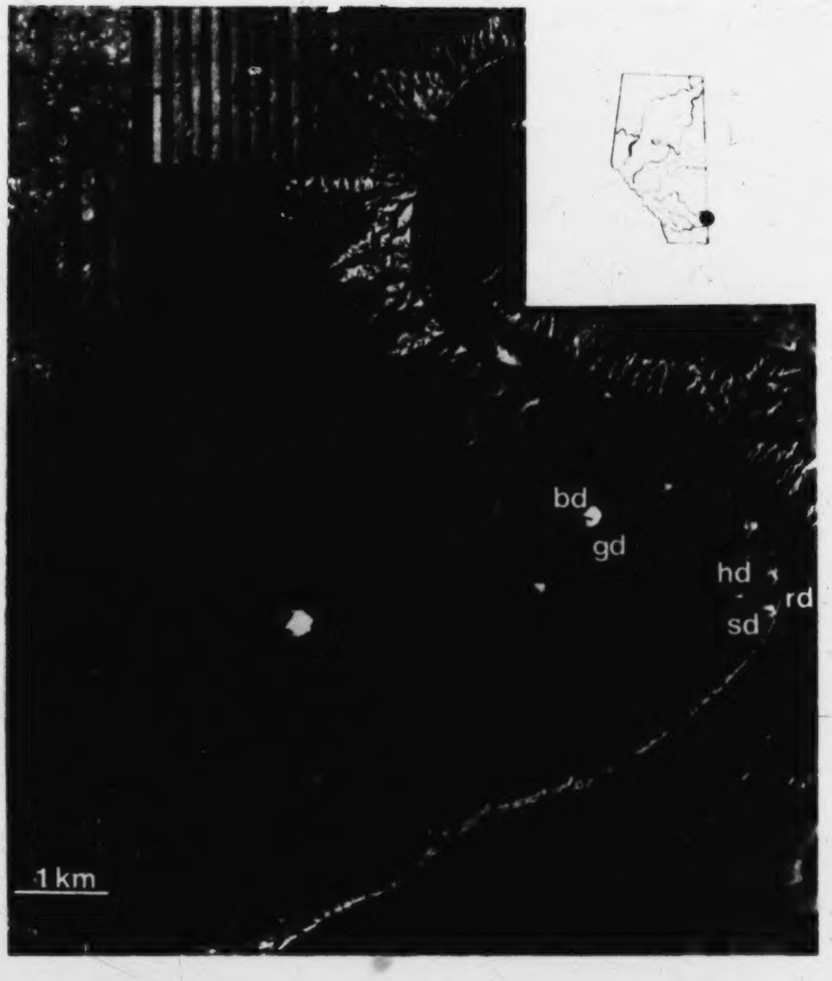
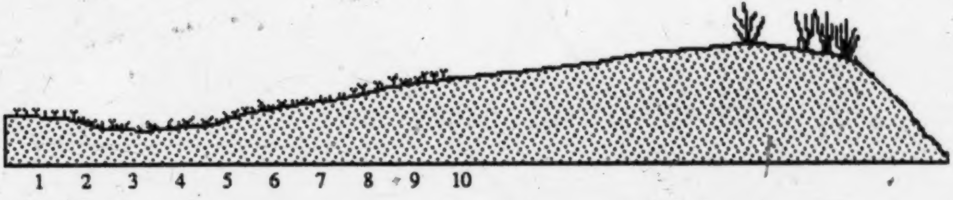
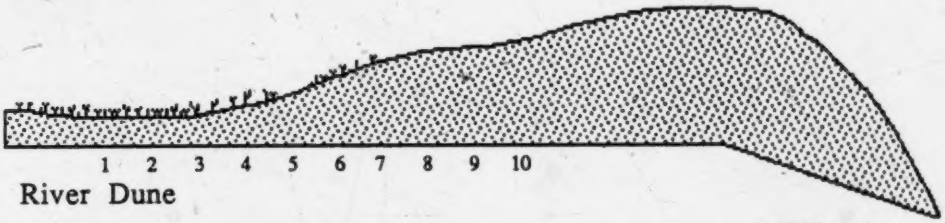

bd
gd
hd
rd
sd
1 km

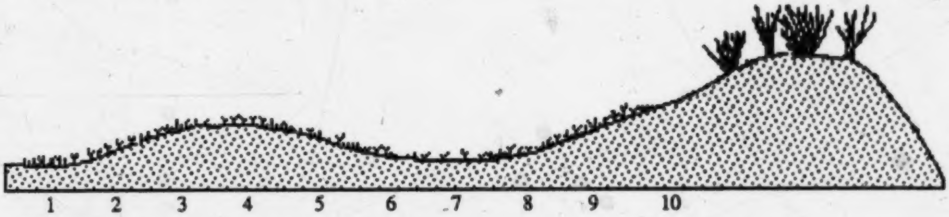
Figure II-1: Diagrammatic cross section of the five dunes used for pitfall trapping, showing location of trap transects. Distance between traps is 5 m.


1
2
3
4
5
6
7
8
9
10

Big Dune


1
2
3
4
5
6
7
8
9
10

River Dune


1
2
3
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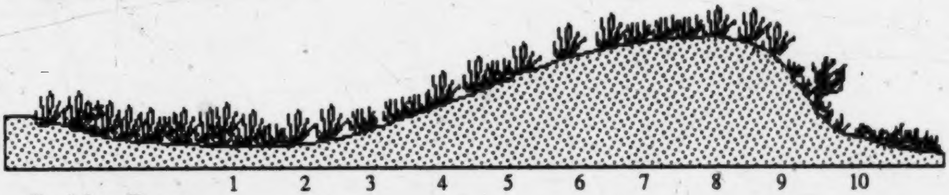
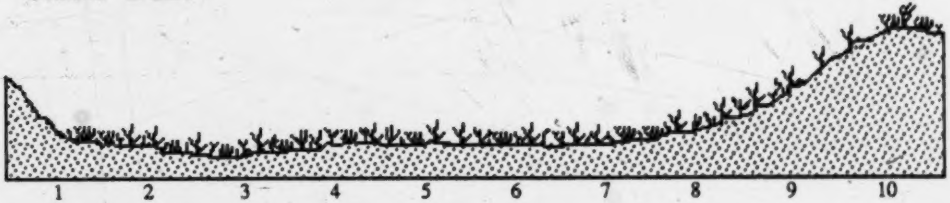
9
10

Home Dune


1
2
3
4
5
6
7
8
9
10

Stable Dune


1
2
3
4
5
6
7
8
9
10

Grassy Dune

Figure II-2: Cluster analysis dividing pitfall trap sites into four habitat types based on presence or absence of plant species. Axis at bottom shows average distance values, based on Jaccard's coefficient of similarity. Trap abbreviations: RD: River Dune, BD: Big Dune, HD: Home Dune, SD: Stable Dune, GD: Grassy Dune.

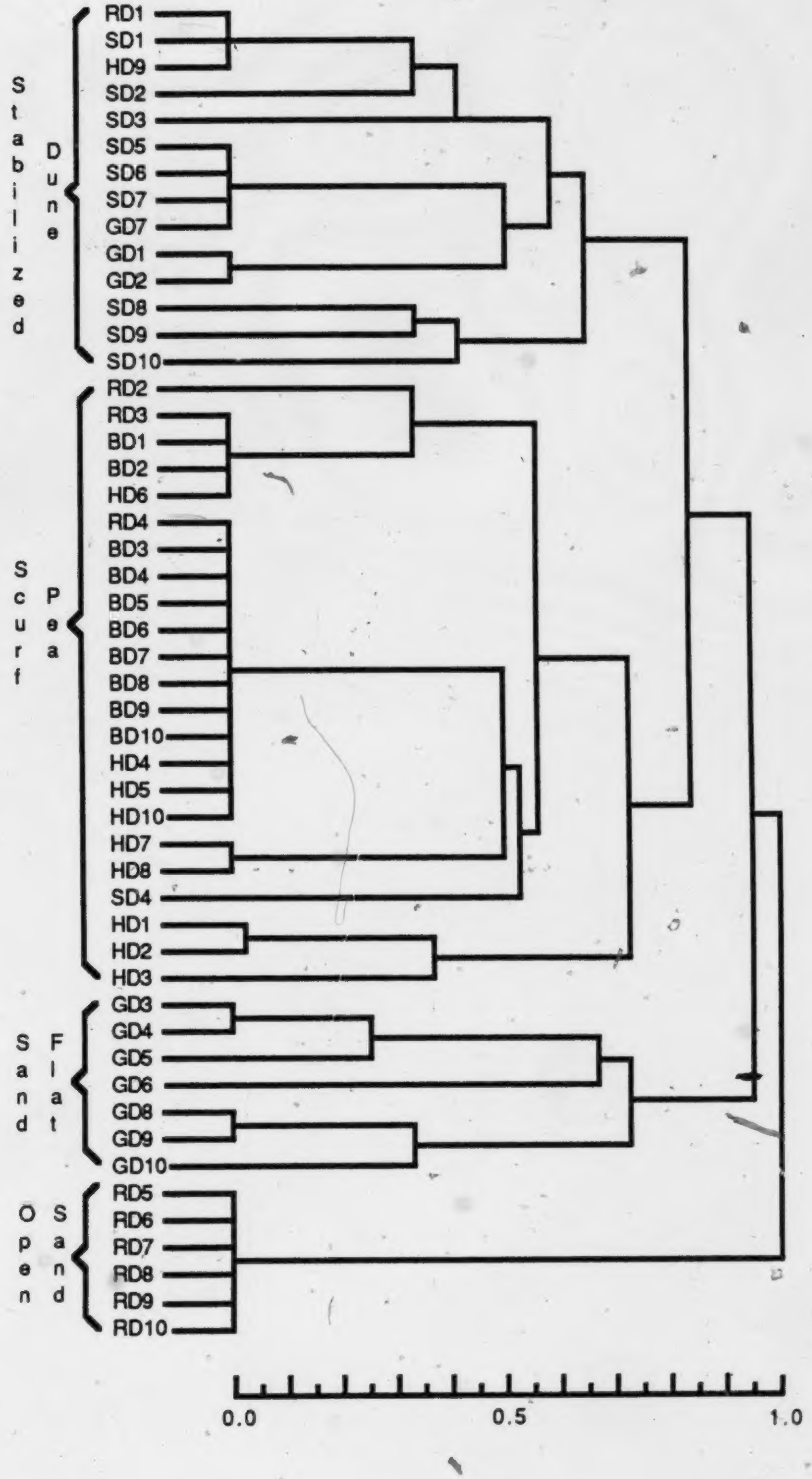
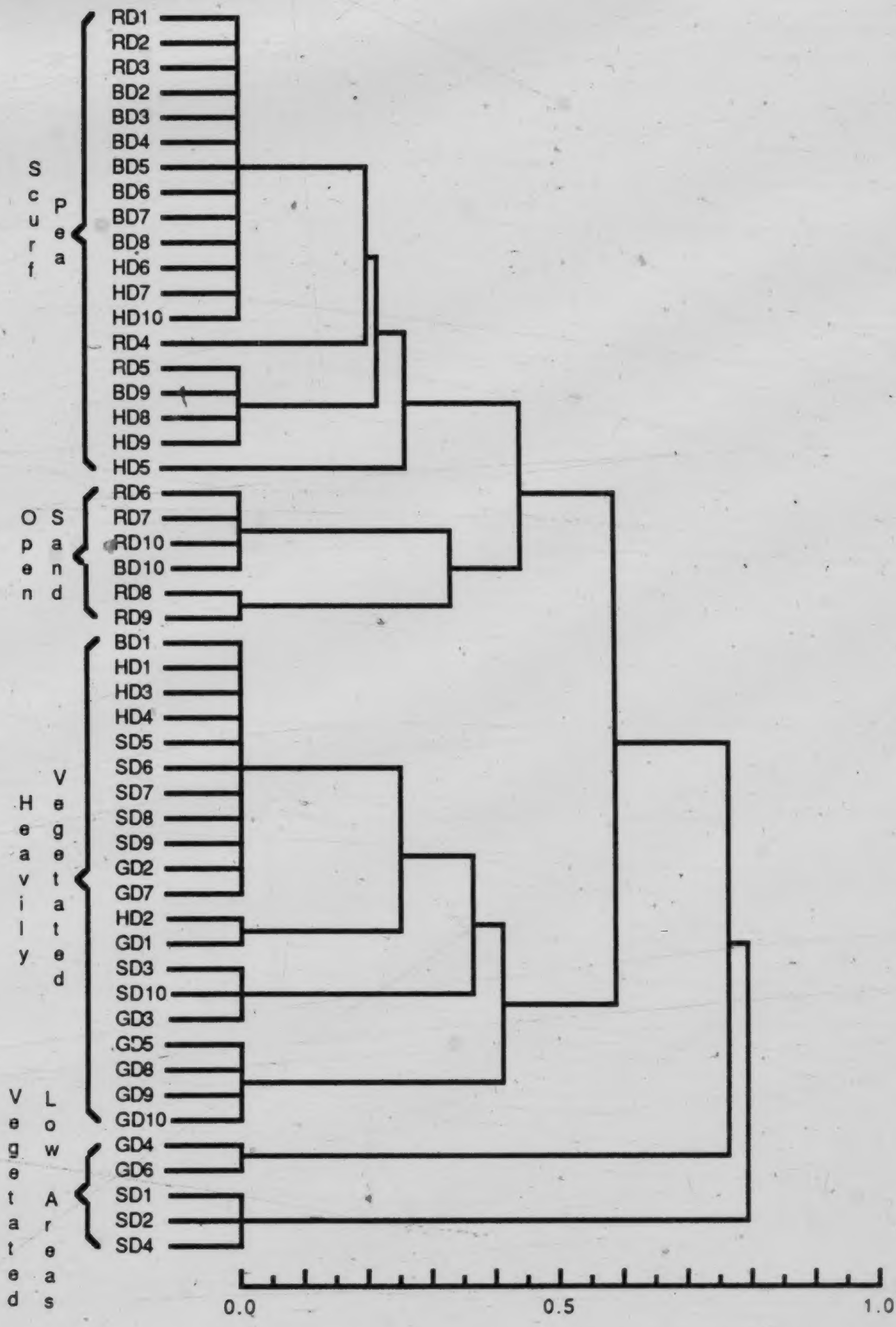
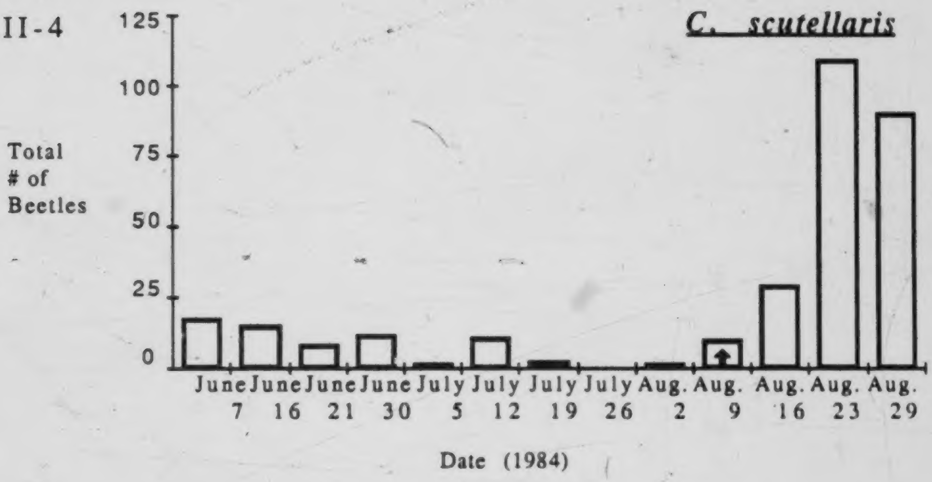

Stabilized Dune
RD1
SD1
HD9
SD2
SD3
SD5
SD6
SD7
GD7
GD1
GD2
SD8
SD9
SD10
Scurf Pea
RD2
RD3
BD1
BD2
HD6
RD4
BD3
BD4
BD5
BD6
BD7
BD8
BD9
BD10
HD4
HD5
HD10
HD7
HD8
SD4
HD1
HD2
HD3
Sand Flat
GD3
GD4
GD5
GD6
GD8
GD9
GD10
Open Sand
RD5
RD6
RD7
RD8
RD9
RD10
0.0
0.5
1.0

Figure II-3: Cluster analysis dividing pitfall trap sites into four habitat types based on presence or absence of *Cicindela* species. Axis at bottom shows average distance values, based on Jaccard's coefficient of similarity. Trap abbreviations: RD: River Dune, BD: Big Dune, HD: Home Dune, SD: Stable Dune, GD: Grassy Dune.

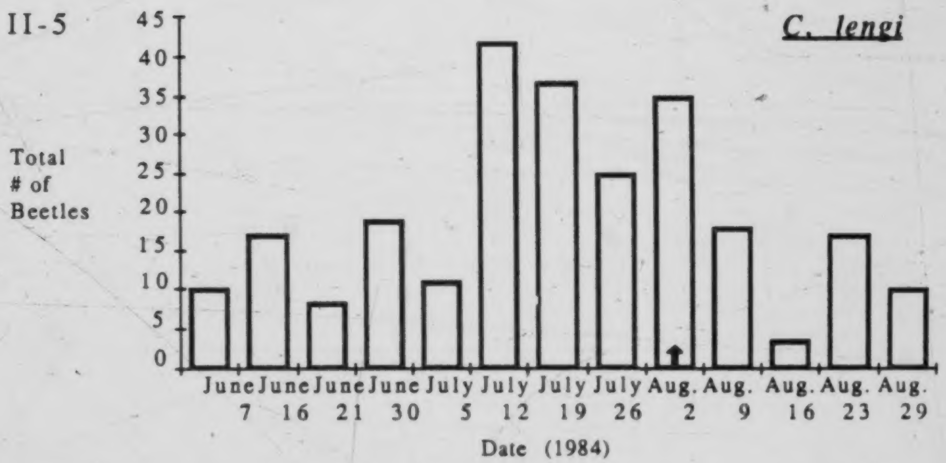

Scurf Pea
RD1
RD2
RD3
BD2
BD3
BD4
BD5
BD6
BD7
BD8
HD6
HD7
HD10
RD4
RD5
BD9
HD8
HD9
HD5
Open Sand
RD6
RD7
RD10
BD10
RD8
RD9
Heavily Vegetated
BD1
HD1
HD3
HD4
SD5
SD6
SD7
SD8
SD9
GD2
GD7
HD2
GD1
SD3
SD10
GD3
GD5
GD8
GD9
GD10
Vegetated Low Areas
GD4
GD6
SD1
SD2
SD4
0.0
0.5
1.0

Figures II-4, II-5: Histograms showing the total number of beetles collected per pitfall trap for each week long sampling period during 1984, for *Cicindela scutellaris* and *C. lengi*. Arrows indicate first emergence of new adults.

II-4

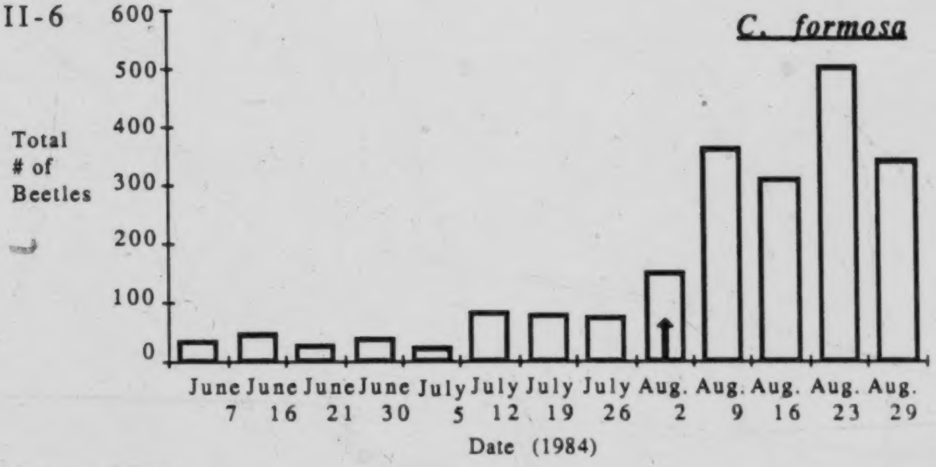

C. scutellaris
Total # of Beetles
125
100
75
50
25
0
June
June 7
June 16
June 21
July 30
July 5
July 12
July 19
Aug. 26
Aug. 2
Aug. 9
Aug. 16
Aug. 23
Aug. 29
Date (1984)

II-5

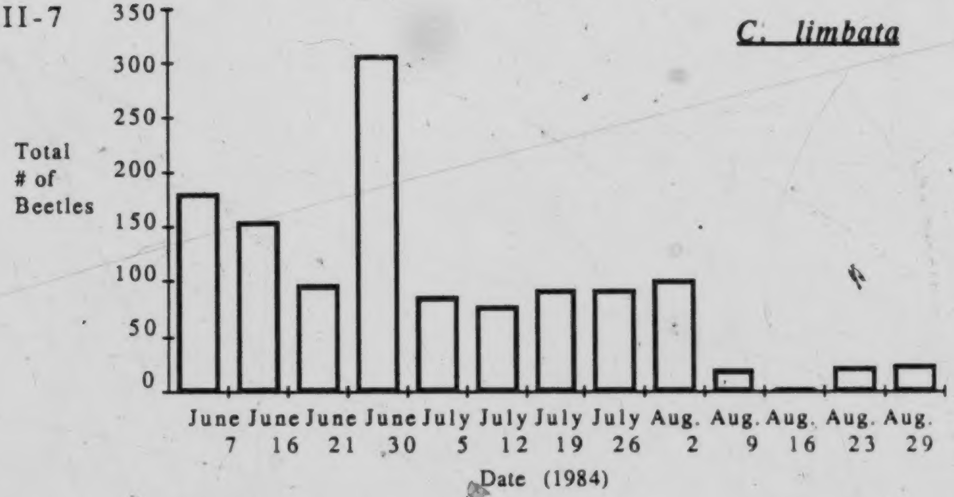

C. lengi
Total # of Beetles
45
40
35
30
25
20
15
10
5
0
June
June 7
June 16
June 21
July 30
July 5
July 12
July 19
Aug. 26
Aug. 2
Aug. 9
Aug. 16
Aug. 23
Aug. 29
Date (1984)

Figures II-6, II-7, II-8: Histograms showing the total number of beetles collected per pitfall trap for each week long sampling period during 1984, for *Cicindela formosa*, *C. limbata*, and *C. lepida*. Arrows indicate first emergence of new adults.

II-6


C. formosa
Total # of Beetles
600
500
400
300
200
100
0
June 7
June 16
June 21
June 30
July 5
July 12
July 19
July 26
Aug. 2
Aug. 9
Aug. 16
Aug. 23
Aug. 29
Date (1984)

II-7


C. limbata
Total # of Beetles
350
300
250
200
150
100
50
0
June 7
June 16
June 21
June 30
July 5
July 12
July 19
July 26
Aug. 2
Aug. 9
Aug. 16
Aug. 23
Aug. 29
Date (1984)

II-8

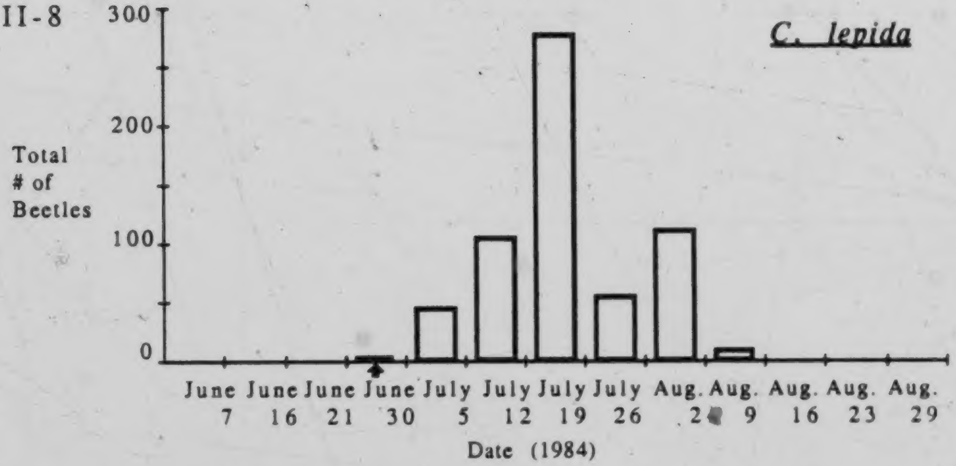
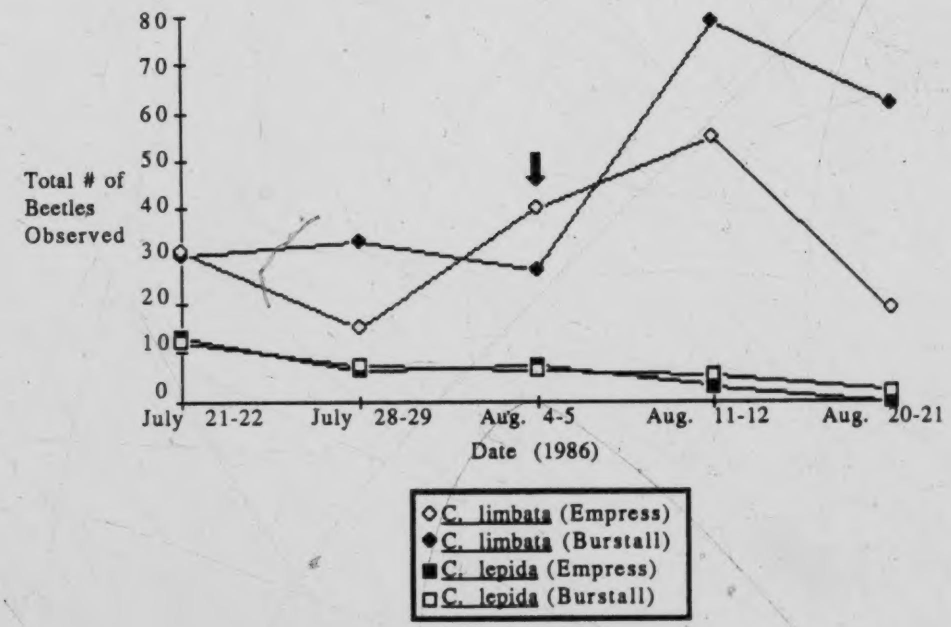

C. lepida
Total # of Beetles
300
200
100
0
June 7
June 16
June 21
June 30
July 5
July 12
July 19
July 26
Aug. 2
Aug. 9
Aug. 16
Aug. 23
Aug. 29
Date (1984)

Figure II-9: Relative abundances of *C. formosa*, *C. limbata* and *C. lepida* at the Empress and Burstall dune fields, determined by standardized observations on predetermined transects. Arrow indicates first emergence of new adult *C. formosa*.


80
70
60
50
40
30
20
10
0
Total # of Beetles Observed
July 21-22
July 28-29
Aug. 4-5
Aug. 11-12
Aug. 20-21
Date (1986)
◇ C. limbata (Empress)
◆ C. limbata (Burstall)
■ C. lepida (Empress)
□ C. lepida (Burstall)

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CHAPTER III

MIMETIC TIGER BEETLES AND THE PUZZLE OF CICINDELID COLOURATION (COLEOPTERA: CICINDELIDAE)*

INTRODUCTION

Tiger beetles are a widespread, speciose group of colourful, active beetles, and thus their colouration (by which I mean both pattern and hue) has received much attention from biologists. However, explanations for the colour patterns of adult diurnal tiger beetles still fail to account for all observed colouration. Townsend (1886) suggested that tiger beetles have developed substrate matching colouration though natural selection, and beautiful bright colours through sexual selection. Shelford (1917) identified a "plan" of those areas of the elytron in which light markings appear, and proposed weakly corroborated generalizations regarding colouration and climate. Willis (1967) and Schultz (1986) hypothesized that the dorsal colouration of adult *Cicindela* is primarily disruptive, resulting from selection by vertebrate visual predators, and Pearson (1985) showed that the orange abdomens of some *Cicindela* are aposematic when exposed in flight. As well, white tarsi or mandibles are used by the males of some species as courtship signals (Pearson, 1988). Nocturnal adults of many plesiomorphic taxa (eg. *Omus, Amblychila*) are uniformly dark brown or black, and are presumably not subject to selection by visual predators.

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* in press in Coleopterists Bulletin

I argue here that the colouration of some tiger beetles is best interpreted as mimetic. It has long been known that some cicindelids serve as models for mimicry: the arboreal Asian tiger beetles *Collyris* and *Tricondyla* are presumably distasteful, and are mimicked by successive instars of the grasshopper *Condylodera tricondyloides* (Westw.), as well as cerambycid beetles and a sciomyzid fly (Shelford, 1902). These tiger beetles are themselves ant-like, and may be mimetic in their own right. A number of other cicindelids have been implicated in mimicry, and these examples are discussed below, along with a summary of what is known about mimicry in cicindelids, and cicindelid colour in general.

A WASP-MIMICKING TIGER BEETLE

This paper presents two new examples of apparently mimetic cicindelids, fortuitously discovered in the course of other work. The first example was uncovered in a display of showy tropical Hymenoptera at the Provincial Museum of Alberta. What I took at first glance to be a misplaced tiger beetle (*Pseudoxychila bipustulata ceratoma* Chaudoir) was in fact a female mutillid wasp, belonging to the genus *Hoplomutilla* Ashmead (Plate III-1a,b). Both exhibit dark ground colour, paired pale abdominal spots, similar body size, and live in open ground habitats in rainforests, and are diurnal (Palmer, 1976, re. the beetle; A. T. Finnamore, pers. comm., re. the mutillid). The mutillid stings, so the hypothesis that the resemblance is mimetic seems reasonable.

In Ecuador, in May of 1987, I found the beetle commonly in montane areas, but not the wasp, and similar observations with respect to *P. tarsalis* Bates, in Costa Rica, came from an anonymous reviewer. This suggests limited seasonal or geographic overlap between these organisms, or that the wasp is less abundant, which in turn suggests Müllerian rather than Batesian mimicry, since for the latter the model must be more abundant than the mimic.

Pearson (1988) has noticed the resemblance between three other sympatric cicindelid/mutillid pairs, involving the cicindelids *Pseudoxychila tarsalis* (in Costa Rica), *Cicindela pulchra* Say (in the southwestern United States, mimicking several *Dasymutilla* species [Pearson, pers. comm.]), and *C. westermanni* Schaum (in southern India).

A BLISTER BEETLE MIMICKING *CICINDELA*

Cicindela scutellaris scutellaris Say lives on the margins of open sand areas in the Great Plains of North America, and may mimic a toxic blister beetle, *Lytta nuttalli* Say (Plate III-1 c,d). Both are iridescent, with the head and pronotum green, and the elytra red-green, although the elytra of *L. nuttalli* vary from red-green to red-purple. Adult *L. nuttalli* range from seven to 21 mm in length, while *C. s. scutellaris* are approximately 13mm long. Both beetles occur throughout the summer (April- October for *C. s. scutellaris* [personal observation]; late May- September for *L. nuttalli* [Selander, 1960]), throughout the Great Plains of North America. *L. nuttalli* adults feed on legumes, including *Psoralea lanceolata* Pursh, a common sand-stabilizing plant in the habitat of *C. scutellaris scutellaris*. Outside the range of *L. nuttalli*, *C. scutellaris* is represented by six subspecies, none of which possess red and green iridescent colouration.

There is good reason to suspect that adult *L. nuttalli* are toxic since, like all adult meloids, they possess the potent toxin cantharidin (Selander, 1960). Whereas the most important predators of tiger beetles are lizards, birds, and asilid flies (Pearson, 1985), the only known predator of adult *L. nuttalli* is the mirid bug *Hadronema militaris* Uhler (Selander, 1960). Captive lizards rejected the black and yellow meloid *L. fulvipennis* Leconte, showing signs of discomfort after attacking them (Pritchett, 1903). However, I have seen a toad (*Bufo hemiophrys* Cope) eat adult *L. viridana* near Devon, Alberta, and Cushny (1901) reported that frogs, chickens, and hedgehogs show some immunity to the effects of cantharidin. Thus, the degree of toxicity of *L. nuttalli* to its potential predators remains unknown, although it is likely high.

OTHER MIMETIC TIGER BEETLES

Since tiger beetles possess pygidial defence glands (Forsythe, 1970; Moore, 1979), instances of mimicry by tiger beetles are probably Müllerian, at least to some extent. In all reported instances, however, the models of mimetic cicindelids are apparently less palatable than the tiger beetles.

An example of Müllerian mimicry involving tiger beetles alone, which has been described but not as such, is the group of sympatric orange-abdomened distasteful *Cicindela* which Pearson (1985) studied in Arizona. Pearson has provided good evidence that the beetles are distasteful, and that their colouration is aposematic. Thus, they may benefit from resembling one another.

A more complex situation involves several South African beetles and female mutillids, in what may constitute three Müllerian assemblages (Marshall, 1902; Cassola, 1986). The first assemblage consists of numerous species of female mutillids, in the genus *Mutilla*; carabids in the genera *Atractonota, Eccoptoptera, Graphipterus, Piezia*, and *Polyhirma*; cicindelids in the genus *Dromica*; and clerid beetles in the genus *Graptoclerus*. The second assemblage involves *Polyhirma* species and *Dromica* species, which resemble one another but not the mutillids. The third set of mimetic resemblances involves the cicindelid *Mantichora*, and adults of some species in the carabid genus *Anthia*, which are similar in habitus and defense behavior. Corroboration of this complex hypothesis must await further field research. However, these systems serve to illustrate that tiger beetles may participate in large mimetic assemblages, reminiscent of the more familiar mimicry systems involving tropical butterflies.

EXPLANATIONS FOR TIGER BEETLE COLOURATION

Four general explanations have been proposed for the function of colouration in adult tiger beetles: crypsis, disruption by iridescence, mimicry, and thermoregulation. Crypsis is inferred when beetles appear to match the colour and patch size of soils on which they live (Schultz, 1986; Willis, 1967). Iridescent colours are disruptive in the sense that it is difficult for predators to visually judge the distance between themselves and iridescent beetles, since both colour and brightness change rapidly with viewing angle. The physics of this phenomenon, where iridescence is produced by plane diffraction gratings, are outlined by Hinton and Gibbs (1971). Although iridescence in tiger beetles is produced by interference reflectors rather than diffraction gratings (Schultz and Rankin, 1985), Schultz (1986) also interprets iridescence as a means to hinder visual tracking by predators, especially of rapidly moving beetles. In other iridescent beetles, however, bright colours can also be aposematic (Hinton and Gibbs, 1971), and I argue here that some tiger beetles are as well. Finally, the extent of light and dark areas on the elytra of *Cicindela* have thermoregulatory consequences, and affect the amount of time an adult beetle can spend foraging or mating on sunlit substrates, as opposed to basking or cooling in shade (Acorn, in prep., Chapter IV).

The colouration of an individual beetle can serve more than one of these functions simultaneously. Adult *C. s. scutellaris* are both mimetic and iridescent, while adult *P. b. ceratoma* are probably just mimetic. The functions of colouration may also differ with distance from a potential predator. At a distance, adult *C. s. scutellaris* appear dark and dull to a human observer, but up close their colours are bright and obvious. Hinton and Gibbs (1971) have suggested that the diffraction gratings of iridescent beetles are imperfect, in the sense that it is possible through the same developmental process to produce gratings which give much brighter colours. They hypothesize that selection has favored colours bright enough to warn predators away at close distances, but not so bright that they attract potential predators from afar. Similar selection pressures may act on tiger beetle colours. Townsend's (1886) suggestion that bright colours are the result of sexual selection can almost surely be discounted, if only because tiger beetles are not sexually dimorphic for colour.

On the other hand, similar colouration may serve very different functions, even within a species. I assume that not all of the seven or so subspecies of *C. scutellaris* are mimetic, yet the adults of many possess bright colours similar to those of *C. s. scutellaris*. Another example is the species *C. formosa* Say. Adult *C. f. pigmentosignata* W. Horn resemble fragments of red-purple sandstone, and both the beetles and the stones show the same geographic range (Schultz, 1986). However, *C. f. formosa*, which differs from the latter subspecies only in red rather than purple colour, and the extent of light elytral markings, is not a mimic of red sandstone patches, and its colouration is perhaps best interpreted as disruptive. *Cicindela formosa gibsoni* Brown has wider light markings than the nominate subspecies, and this affects its thermoregulatory behavior: it can forage longer in the heat, but must bask longer in cool conditions (Acorn, in prep., Chapter IV).

It is difficult to determine the function of colouration in a given taxon without knowing something about the organism's behaviour and environment. Even so, mimicry may be quite widespread in the Cicindelidae. Since mimicry is uncommon in carabid beetles (with a few exceptions, such as some species in the genus *Lebia*, adults of which mimic alticine chrysomelids [Lindroth, 1971] and some adult *Agra*, which may mimic sympatric brentid weevils [Erwin, 1986]), it is possible that workers on this group may overlook examples. Our understanding of tiger beetle colouration is improving but, as coleopterists, we should not be discouraged when our efforts to understand are thwarted by the very thing for which beetles are best known- diversity.

ACKNOWLEDGEMENTS

I would like to thank D. J. Brothers for identifying the mutillid. Helpful comments on the manuscript came from G. E. Ball, L. Shortreed, D. L. Pearson, T. D. Schultz, T. G. Spanton, J. R. Spence, D. A. Wrubleski, and two anonymous reviewers. This work was supported by grants to J. R. Spence from the National Science and Engineering Research Council of Canada.

Plate III-1. Mimetic tiger beetles and their models: a) *Pseudoxychila bipustulata ceratoma*, Leticia, Columbia; b) *Hoplomutilla* sp., female, Quiroz, Rio Paucartambo, Peru; c) *Cicindela scutellaris scutellaris*, dunes south of Empress, Alberta, Canada; d) *Lytta nuttalli*, dunes south of Empress, Alberta, Canada. Scale bar= 1 cm.

THE QUALITY OF THIS MICROFICHE IS HEAVILY DEPENDENT UPON THE QUALITY OF THE THESIS SUBMITTED FOR MICROFILMING.

UNFORTUNATELY THE COLOURED ILLUSTRATIONS OF THIS THESIS CAN ONLY YIELD DIFFERENT TONES OF GREY.

LA QUALITE DE CETTE MICROFICHE DEPEND GRANDEMENT DE LA QUALITE DE LA THESE SOUMISE AU MICROFILMAGE.

MALHEUREUSEMENT, LES DIFFERENTES ILLUSTRATIONS EN COULEURS DE CETTE THESE NE PEUVENT DONNER QUE DES TEINTES DE GRIS.

A
B
C
D

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CHAPTER IV

THERMOREGULATORY CONSEQUENCES OF ELYTRAL PATTERN FOR DUNE *CICINDELA* (COLEOPTERA: CICINDELIDAE)

INTRODUCTION

Sand dune habitats are subject to great extremes of temperature (Chapman *et. al.*, 1926), but sand dune tiger beetles, in the genus *Cicindela*, have evolved numerous thermoregulatory mechanisms to keep their body temperatures within a narrow range while they are active (Dreisig, 1980; Guppy *et. al.*, 1983; Morgan, 1985). Adult *Cicindela* increase their body temperature by basking, and reduce or stabilize it by moving into shade, stilting (holding the body high off the ground), taking short flights for convective cooling, and by digging into the sand. Their thermoregulatory time budgets can be predicted by a general model, which has been shown to apply to both tiger beetles and diurnal lizards (Dreisig, 1985).

In this paper, I test the hypothesis that colouration affects thermoregulation in adult *Cicindela limbata* Say and *C. formosa* Say. Both species are common in open, sandy habitats, such as the margins of open sand dunes, in the Great Plains, and both include populations with light coloured elytra, which at first glance one would easily attribute to crypsis. However, elytral colour may affect thermoregulation by determining the relative absorbance of solar radiation by beetles. So, crypsis and thermoregulation both offer reasonable explanations for the elytral patterns of these beetles.

Adult tiger beetles show a tremendous variety of colour patterns both among and within species, with some species showing geographic colour and pattern variation and some populations exhibiting colour polymorphism.

The hypothesis that colour affects thermoregulation seems reasonable, since dark surfaces generally absorb the infrared portion of solar radiation better than light reflective surfaces. Burtt (1981) predicts uniformly light colour for uninsulated terrestrial animals which frequently encounter the need to reduce body temperature. However, in birds and mammals, dark feathers or fur can impede radiation penetration to the skin surface, and energy can be lost to the environment rather than being transmitted to the organisms' body, such that light feathers or fur counterintuitively act to improve solar warming (Walsberg, 1983). Since the elytra and folded hind wings of adult *Cicindela* may also serve as insulation (Van Natto and Freitag, 1986), it is difficult to predict the effect of elytral colour on thermoregulation, and in fact no good evidence has surfaced to suggest that tiger beetle colouration is related to thermoregulation. For a review of the rather confusing and contradictory literature on colouration and thermoregulation in insects in general, see Casey (1981).

I argue below that light colour (expanded light markings) is a thermoregulatory adaptation for beetles in open, upland habitats where very high temperatures are commonplace. Most *Cicindela* in these habitats live on bare expanses of sand or saline soil, and most of these beetles have expanded light markings (Chapter V; Willis, 1967). On light sand or saline soils, however, these colour patterns also enhance substrate matching, and thus the consequences of expanded markings may be both reduced predation and increased ability to remain active at high temperatures.

It has been suggested (Dreisig, 1980) that selection has favoured so-called maxithermal adaptations (maintenance of body temperature near the upper tolerance threshold) in tiger beetles. For *C. hybrida*, in dry sand habitats in Denmark, predation efficiency is highest at high body temperatures, while abundance of prey increases with ambient temperature (Dreisig, 1980, 1981). Striking similarity of upper lethal temperatures among adult *Cicindela* of various species suggests an upper physiological limit to maxithermal adaptation (Pearson and Lederhouse, 1987). Slight differences in ability to forage below this upper threshold may well have consequences for an individual's fitness, since prey are a limiting resource for at least some tiger beetles (Pearson and Knisley, 1985). Thus, it is reasonable to suspect that thermoregulatory selection pressures have been of importance in tiger beetle evolution.

MATERIALS AND METHODS

In this paper, "colouration" refers to both the darker background colour of the integument of adult *Cicindela*, and the pattern of light and dark elytral markings. These two aspects of colouration are referred to as "colour" and "pattern" respectively, and the term "colouration" is here a synonym for "colour pattern." Light markings have been given names in the tiger beetle literature, although "markings" refers, in most other areas of biology, to areas with pigment or dark structural colour. Thus, in the study of tiger beetles, "markings" can refer to either light or dark areas. Light markings usually take the form of lunules or sigmoid bands, which in some species are reduced to spots, and in others are expanded and fused into large white areas. In *C. limbata* and *C. formosa* both expanded and reduced light markings are present in different areas of these species' geographic ranges (Figs. IV-1).

For comparisons of beetles within subspecies, I estimated the proportion of the left elytron covered by dark markings using a camera lucida and an Apple II Plus microcomputer with a digitizing tablet. This proportion is the property which is hypothesized to affect thermoregulation. In comparisons between subspecies, this measurement was omitted, since the subspecies involved showed little or no overlap with respect to elytral pattern, one subspecies having relatively expanded light markings in comparison with the other.

The hypothesis that elytral pattern affects thermoregulation, and thus beetle activity, was tested on three different time scales: 1) seasonal activity, 2) diel activity patterns, and 3) in terms of time spent shuttling between foraging, basking, and cooling in the shade. Statistical analyses were performed on the mainframe Amdahl 5870 computer at the University of Alberta, using the Midas statistical program (Fox and Guire, 1976).

Warming and Cooling Rates

Warming and cooling rates were compared in the laboratory between subspecies of both *C. limbata* and *C. formosa*. Ten adults were used of *C. limbata hyperborea* LeConte (with non-expanded light markings), *C. limbata nympha* Casey (with expanded light markings), *C. formosa formosa* Say (with non-expanded light markings) and *C. formosa gibsoni* Brown (with expanded light markings). Specimens were killed by freezing, and a thermistor probe was inserted through a small incision in the mesosternum, sealed with vaseline.

Specimens were used one at a time, and subspecies were alternated throughout the experiment. Beetles were then heated by a focussed dissecting microscope light at a distance of 10 cm. Once the specimen reached a maximum temperature, the light was turned off. Changes in temperature were recorded on a Grant portable chart recorder. The time required to warm the specimen from 25 °C to 35 °C was taken from the chart record, as was the time required to cool from 35 °C to 25 °C once the light was turned off. Maximum equilibrium temperatures fluctuated somewhat, and so were not used in the warming/cooling calculations.

Specimens of *C. limbata* were collected at Nestow (*C. limbata nympha*) and Fort McKay, Alberta (*C. limbata hyperborea*) on May 24-25, and the experiment was performed with them on May 28, 1986 after keeping the beetles in a terrarium. Specimens of *C. formosa* were collected at Empress, Alberta (*C. formosa formosa*) and Fox Valley, Saskatchewan (*C. formosa gibsoni*) on August 19-20, 1986, and the experiment was performed with them on September 12, 1986, after keeping the beetles alive in refrigeration.

Size differences between subspecies, which could confound the results, were tested for by comparisons (Students *t*-test) of length (from the elytral apex to a line tangent to the front of both eyes).

Seasonal Activity and Elytral Pattern

To assess the effect of elytral pattern on ability to maintain activity seasonally, twenty adult *C. limbata nympha* were collected each week at a sandy blowout near Nestow, Alberta, from August 24 to October 11, 1985 (only six were collected on the latter date). The sample population was divided into three categories with respect to proportion of dark elytral area, delineated by points one half of the standard deviation from the mean. A *G*-test was performed to determine whether elytral pattern was independent of date of capture. A correlation matrix was generated among values for sex, date, temperature, total elytral area, and percent dark elytral area.

Diel Activity and Elytral Pattern

C. limbata nympha were collected throughout the day on June 14 and June 21, 1985, to determine the effect of elytral pattern on activity. Beetles were netted and placed in waxed paper envelopes, with the time of collection written on the outside of the envelope. This work was done on the Empress dunes, along the border between southern Alberta and Saskatchewan (see Chapter II for description of this site). Throughout both days, at 30 minute intervals, a number of environmental factors were measured. Three thermistors, connected to a Grant portable chart recorder, were used to measure temperature one meter above ground, shaded by a white plastic container; on the sand surface; and 2.5 cm below the sand surface. Incoming solar radiation was measured by means of an Archer infrared detecting diode, and an Archer cadmium sulfide photo cell, the latter sensitive primarily to visible light, with peak sensitivity in the yellow to green range (500-600 nm, according to manufacturer's specifications). Both were mounted on a small plastic box, and changes in D.C. resistance were measured on a Micronta model 22-212 multimeter, in KV, on a logarithmic scale. Thus, only a relative measure of light intensity was obtained.

Contingency tables were constructed for each day, with numbers of beetles collected during half hour intervals pooled to give a minimum expected value in each cell of five. Then, *G* -tests were performed to determine whether proportions of the sample population in each pattern category were independent of time of capture. A correlation matrix was generated among values for number of beetles collected per unit time, air temperature, sand surface temperature, subsurface temperature, infrared radiation and visible solar radiation.

Thermoregulatory Time Budgets and Elytral Pattern

Thermoregulatory time budgets were compared between light and dark adults of both *C. limbata* and *C. formosa*. Beetles were first prevented from flying by fastening their wings shut with cyanoacrylate glue. Then, a light and a dark beetle were released in typical habitat, each followed by an observer carrying a digital watch and a notepad. Beetle behaviour was classified as heat stress behaviour (stopping in shade, digging, climbing plants), warming behaviour (basking), or near equilibrium behaviour (foraging, mating, feeding). Because it was difficult to consistently identify, and because it results from low levels of thermal stress, stilting was not recorded as such.

The beetles showed no inclination to flee the observers after a short initial period. Each pair of beetles was observed for between 15 and 60 minutes. Specimens of *C. limbata* were collected at Nestow (*C. limbata nympha*) and Fort McKay, Alberta (*C. limbata hyperborea*) on May 24-25, and observed at Nestow on

June 10, 1986. Specimens of *C. formosa* were collected at Empress, Alberta (*C. formosa formosa*) and Fox Valley, Saskatchewan (*C. formosa gibsoni*) on August 17, 19, and 20, and observed at Empress (1 hour) on Aug. 19, at Burstall, Saskatchewan (1 hour) on Aug 21, and at Nestow (2.25 hours) on Aug 27, 1986. Although Nestow is outside the range of *C. formosa*, the habitat is physically similar to that occupied by this species further south, although plant species differ. *G*-tests were performed to determine whether the proportions of beetles in the three behavioural categories were independent of elytral pattern (i.e. subspecies).

RESULTS

Warming and Cooling Rates

Significant differences in both warming and cooling rates were found between subspecies of *C. limbata* (Table IV-1). For *C. formosa*, the data appear to show the same trend as for *C. limbata*, but the differences are not significant, possibly due to high variance. For *C. limbata* these differences corroborate the prediction that darker beetles warm more quickly, and that different thermal properties of differently patterned elytra can affect internal thoracic temperatures. The results of subsequent time budget experiments, in which both species show thermoregulatory differences between colour morphs, suggest that there must be significant warming differences between subspecies of both species, even if these differences were not detected here. In neither pair of subspecies was there a significant difference in body length, so differences in warming and cooling rates are not simply a consequence of size.

The significant difference in cooling rate between subspecies of *C. limbata* was surprizing, and cannot be attributed to differences in colour, which are not expected to affect cooling rate. These differences could be the result of different surface area to volume ratios, but I can see no structural differences between the subspecies other than colouration. Possibly there are differences in the surface of the cuticle, detectable only with electron micrography. Again, for *C. formosa*, the data appear to show the same trend as for *C. limbata*, but the differences are not significant.

Seasonal Activity and Elytral Pattern

Proportions of the three pattern classes were independent of capture date, and thus elytral pattern was not related to seasonal activity in *C. limbata* (Table IV-2). Elytral pattern was not significantly correlated with date, sex, elytral area, or temperature. Highly significant correlations were found between sex and elytral area ($r = 0.48$, $p < 0.01$), and date and temperature ($r = -0.88$, $p < 0.01$) indicating that males are smaller than females, and that temperature drops in the fall. Less significant correlations were observed between sex and date ($r = -0.27$, $p < 0.05$), temperature and sex ($r = 0.24$, $p < 0.05$), and elytral area and temperature (r=

0.23, $p < 0.05$), but not elytral area and date ($r = -0.17$, $p < 0.05$). This indicates a tenedency for males (which are smaller than females) to remain acitive later in the fall.

Diel Activity and Elytral Pattern

Proportions of the three pattern classes were independent of time of capture for both days (Table IV-3). Therefore, I reject the hypothesis that darker or lighter beetles would predominate during the early or late part of the activity period, or during the warmest part of the day, around 1400 hr. For both days, all environmental variables (three measurements of temperature and two of solar radiation) were strongly correlated with one another ($p < 0.001$), increasing until c. 1400 hr, and decreasing thereafter. Beetle activity began around 730 hr both days, and ended by 2100 hr on June 14 (a warm, sunny day throughout) and around 1400 hr on June 21 (sunny morning, afternoon rain). For pooled data from both days, the number of beetles collected per hour was loosely correlated with air temperature ($r = 0.15$, $p < 0.05$) and more strongly correlated with sand surface temperature ($r = 0.59$, $p < 0.01$), and subsurface temperature ($r = 0.30$, $p < 0.01$). Number of beetles collected per hour was also correlated with visible solar radiation ($r = -0.40$, $p < 0.01$) and infrared radiation ($r = -0.36$, $p < 0.05$). The r values are negative for these radiation measures since the measure itself (D.C. resistance) is inversely related to the magnitude of the radiation. Diel changes in behaviour corresponded to those observed by Dreisig (1980) for *C. hybrida* L.

Thermoregulatory Time Budgets and Elytral Pattern

For both species, significant differences were found between subspecies with respect to thermoregulatory time budgets (Table IV-4). For *C. limbata*, observed during warm, sunny weather, when none of the beetles exhibited basking behaviour, the lighter beetles were able to spend more time foraging, and less cooling than the darker beetles. For *C. formosa*, lighter beetles spent more time basking in cool weather, and less cooling in hot weather than darker beetles. Under the conditions of the experiment, there was no appreciable difference in foraging time between subspecies of *C. formosa*, presumably because foraging time represents the sum of foraging during warmer periods when some beetles were forced to cool themselves, and cooler periods when some beetles were basking. If either warm or cool conditions prevailed in the habitats of these beetles, one colour morph might have a thermoregulatory advantage. In general, for both species, differences in elytral pattern were reflected in behavioural differences in accordance with the prediction that darker beetles warm more readily by infrared absorption.

Light beetles are at an advantage in warmer microenvironments. Southern populations of *C. limbata* are lighter than those in the boreal forest, and would presumably encounter warmer conditions. It is possible that *C. formosa gibsoni* on large dunes in the Great Sand Hills of Saskatchewan experience warmer conditions than populations of *C. f. formosa* on small open sand areas further south, but this is purely speculative.

DISCUSSION

These results demonstrate that colouration affects thermoregulation in at least two species of dune tiger beetles, and that this effect acts on thermoregulatory time budgets rather than on diel or seasonal activity. Beetles at a relative thermoregulatory disadvantage because of their elytral colouration do not become or remain inactive, they simply spend more time in purely thermoregulatory behaviour.

Further evidence for the importance of colouration to thermoregulation may be seen in the interesting correlation between colouration and diel activity pattern in the sympatric Arizona tiger beetles *C. marutha* Dow and *C. fulgoris* Casey. Adults of these two species show diel segregation whereby *C. marutha* is inactive during the heat of the day. As I have argued in Chapter II, this pattern can be parsimoniously interpreted as an adaptation for prolonged foraging in *C. marutha*, rather than as selection by predators and competitors acting indirectly through colouration to acheive diel segregation, as suggested by Pearson and Lederhouse (1987).

Structural features other than colour, such as long legs, white (usually ventral) setae, and small body size may also improve thermoregulation at high temperatures. Long legs increase the height above the substrate during normal locomotion, and the maximum height possible when stilting. White setae (on adults of many species of *Cicindela* which live on sand or salt flats) may serve as reflective surfaces to reduce heat loads (Darlington, 1980). In grassland habitats in Arizona, large body size apparently determines the diel activity pattern of some tiger beetles such that they avoid bird predators and synchronize activity with large prey items (Pearson and Lederhouse, 1987). This seems plausible, although birds prefer large tiger beetles to smaller ones (Pearson, 1985), so selection by birds should not promote increased body size.

Many tiger beetles in dry sand habitats in low latitudes possess all of the features associated above with thermoregulation at high temperatures. As an example, *C. tenuipes* Fab. adults possess expanded markings, extremely long legs, dense white ventral setae, and a relatively small body (Plate IV-1 e). These beetles are found on beach sand in Indonesia (A. T. Finnamore, pers. comm.), and are no doubt subject to very high ambient temperatures. The North American beach dune species *C. dorsalis* Say shows similar but less pronounced features, and along the Atlantic coast shows a north to south trend in reduction of dark elytral pigment, body size, and body size relative to femur length (Boyd and Rust, 1982).

Also with respect to tiger beetle structure and thermoregulation, Van Natto and Freitag (1986) have proposed a functional analogy between tiger beetle bodies and thermos bottles, based on the assumption that iridescent colours of both the elytra and abdominal tergites reduce absorption of infrared radiation (re-radiated by objects in the environment) by reflection, while the sub-elytral airspace insulates against heat uptake through convection and conduction. There are two problems with this idea. First, they present no convincing evidence that absorption of thermal radiation is reduced by reflectance. Second, they assume that "metallic" colours (actually multi-layered interference reflectors [Mossakowski, 1979]) behave like real metals with respect to thermal properties, and thus reflect long wave infrared radiation. This argument is not in agreement with the current belief that "biological tissue, regardless of colour, absorbs all incident thermal [i.e. re-radiated long wave infrared] radiation" (Burtt, 1981).

Tiger beetles thermoregulate by choice of microhabitats, and this has been well documented. They show three behavioural phases as ambient temperature increases; initial shuttling between basking and foraging is followed by graded thermoregulation, and shuttling between shade and sunlight (Dreisig, 1985). Variation among taxa with respect to colour and structure, which affect body temperature and modify the amount of time spent in various microhabitats, should also be considered in general explanations of the thermoregulatiory adaptations of adult *Cicindela*.

The various factors involved in thermoregulation for adult diurnal tiger beetles in open, sunny habitats are summarized in

Figure IV-1.

Whether these thermoregulatory effects are the direct result of thermoregulatory selection pressures, or a consequence of selection for substrate matching is unknown, but it is likely that both factors are involved. The function of colouration in tiger beetles is perhaps best studied on a species by species basis, even though tiger beetle structure is remarkably conservative, making generalizations about functions seem within easy reach. Substrate matching, crypsis, mimicry, and phylogenetic history can all affect colouration, and to distinguish between these causes requires familiarity with the natural history of each species considered. For the sand dune *Cicindela* of the Canadian prairies, I hope I have achieved this familiarity, but much work remains before a general understanding of tiger beetle colouration is reached.

ACKNOWLEDGEMENTS

I very much appreciate voluntary field assistance by L. Shortreed and G. Ogilvie, and technical help from M. MacIntyre. Valuable suggestions and discussion came from G. E. Ball, D. L. Pearson, J. Roland, T. D. Schultz, J. R. Spence, and F. A. H. Sperling, as well as numerous members of the Entomology and Zoology Departments of the University of Alberta. The Fowlie family kindly allowed me to work and camp on their land at Empress. This work was supported by grants to J. R. Spence from the National Science and Engineering Research Council of Canada.

CICINDELA LIMBATA	Warming, from 25 to 30°C	Cooling, from 30 to 25°C
C. limbata hyperborea (dark)	13.08 ±2.7 s	108.0 ±15.9 s
C. limbata nympha (light)	17.7 ±3.73 s	76.8 ±18.78 s
Test Statistic	T= 3.178	T= -3.971
Significance	P< 0.01**	P< 0.001**
CICINDELA FORMOSA		
C. formosa formosa (dark)	30.9 ±6.62 s	87.0 ±3.0 s
C. formosa gibsoni (light)	33.7 ±8.6 s	86.4 ±14.0 s
Test Statistic	T= -0.732	T= 0.104
Significance	(not significant)	(not significant)

Table IV-1. Warming and cooling times, in seconds (mean ± standard deviation) for light and dark tiger beetles.

Date (1986)	Number of individuals in each pattern category (% dark markings)			
	light	medium	dark	
	14.3-22.7%	22.8-26.7%	26.8-33.2%	totals
Aug. 24	6	10	4	20
Sept. 4	7	7	6	20
Sept. 14	3	8	9	20
Sept. 25	7	8	5	20
Sept. 30, Oct. 11	8	6	12	26
totals	31	39	36	106
	G= 7.34 (not significant)			

Table IV-2. Frequencies of elytral pattern categories over a seven week period at Nestow, Alberta. *(C. limbata nympha)*

Time	Number of individuals in each pattern category (% dark markings)			
	light	medium	dark	totals
(June 14, 1985)	12.7-21.9%	22.0-25.9%	26.0-35.3%	
7:00-10:00	6	12	10	28
10:00-11:00	8	8	9	25
11:00-12:00	7	9	8	24
12:00-14:00	6	9	6	21
14:00-16:00	4	13	4	21
16:00-17:00	7	10	7	24
17:00-21:00	10	14	10	34
totals	48	75	54	177
	G= 5.25 (not significant)			
Time	light	medium	dark	totals
(June 21, 1985)	15.4-23.0%	23.1-27.0%	27.1-35.0%	
7:00-11:00	11	10	15	36
11:00-12:00	7	13	3	23
12:00-14:00	9	16	6	31
totals	27	39	24	90
	G= 8.63 (not significant)			

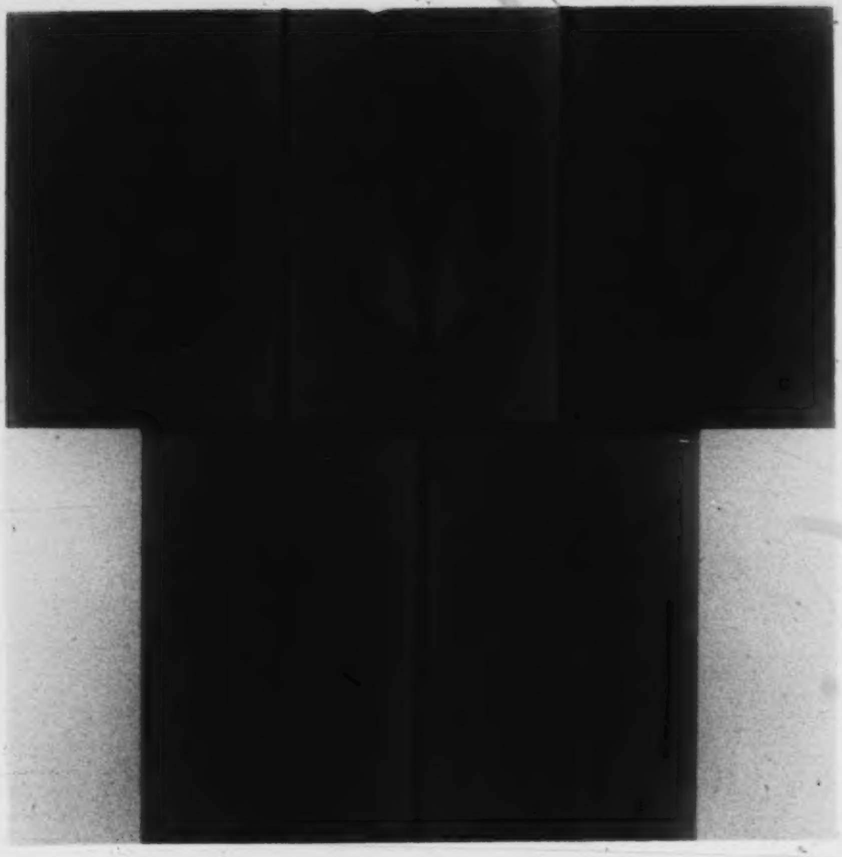
Table IV-3. Frequencies of elytral pattern categories during two days at the Empress sand dunes, Alberta. *(C. limbata nympha)*

		Behavioural Categories:			
CICINDELA LIMBATA		Bask	Forage/Stilt	Shade/Dig	Total
C. limbata hyperborea	(dark)	- -	1206	5994	7200
C. limbata nympha	(light)	- -	1732	5468	7200
	Total:	- -	2938	11462	14400
	G= 118.81 P< 0.001**				

CICINDELA FORMOSA		Bask	Forage/Stilt	Shade/Dig	Total
C. formosa formosa	(dark)	3916	5426	3980	13322
C. formosa gibsoni	(light)	4370	5408	3544	13322
	Total:	8286	10834	7524	26644
	G= 50.21 P< 0.001**				

Table IV-4. Thermoregulatory behaviour in light and dark tiger beetles (figures represent time, in seconds, spent exhibiting each behavioural category).

Plate IV-1. Tiger beetles mentioned in the text: a) *Cicindela formosa formosa*, b) *C. f. gibsoni*, c) *C. limbata nympha*, d) *C. l. hyperborea*, e) *C. tenuipes*. Scale bar = 1 cm.



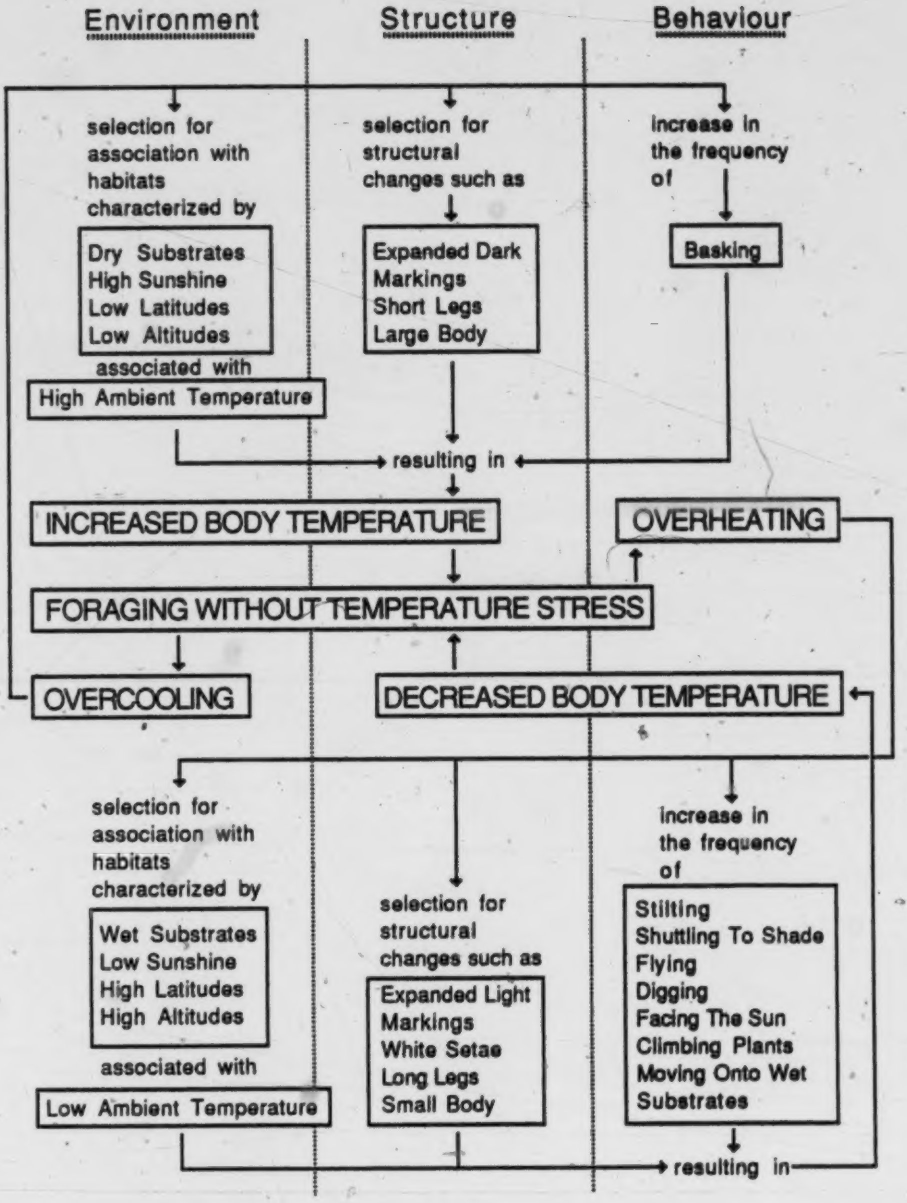

Environment
Structure
Behaviour
selection for association with habitats characterized by
Dry Substrates
High Sunshine
Low Latitudes
Low Altitudes
associated with
High Ambient Temperature
selection for structural changes such as
Expanded Dark Markings
Short Legs
Large Body
increase in the frequency of
Basking
resulting in
INCREASED BODY TEMPERATURE
OVERHEATING
FORAGING WITHOUT TEMPERATURE STRESS
OVERCOOLING
DECREASED BODY TEMPERATURE
selection for association with habitats characterized by
Wet Substrates
Low Sunshine
High Latitudes
High Altitudes
associated with
Low Ambient Temperature
selection for structural changes such as
Expanded Light Markings
White Setae
Long Legs
Small Body
increase in the frequency of
Stilting
Shuttling To Shade
Flying
Digging
Facing The Sun
Climbing Plants
Moving Onto Wet Substrates
resulting in

Figure IV-1. Factors involved in thermoregulation for adult diurnal tiger beetles in sunlit habitats.

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Chapter V

THE HISTORICAL DEVELOPMENT OF GEOGRAPHIC COLOUR VARIATION AMONG DUNE *CICINDELA* IN WESTERN CANADA (COLEOPTERA: CICINDELIDAE)

INTRODUCTION

Nine species of *Cicindela* live on open sand dunes in western Canada. Five of these (*C. limbata* Say, *C. formosa* Say, *C. scutellaris* Say, *C. lengi* W. Horn, and *C. lepida* Dejean) are regularly found together in suitable habitats in the Canadian prairies (Chapter II). In addition, *C. hirticollis* Say lives on dunes adjacent to water, *C. longilabris* lives on dunes and open sandy soil in forested regions (particularly among pines and other conifers), and *Cicindela duodecimguttata* Dejean and *C. tranquebarica* Herbst live on dunes as well as other open ground habitats.

In this paper, I concentrate on two questions regarding colour variation among these beetles. First, why have beetles living in what appear to be physically simple habitats evolved a diversity of colour patterns? Second, to what extent can historical biogeographic hypotheses aid in interpretation of the present pattern of intraspecific geographic variation in these beetles?

The colours of tiger beetles, coupled with their active habits, have made them popular with amateur entomologists. Tiger beetle colouration has also attracted attention from biologists interested in its function and origin. After detailed study, Shelford (1917) concluded that all tiger beetle elytral patterns were derived from combinations of 28 spots produced by the confluences of seven transverse and four longitudinal bands, and constructed a number of complex transition series linking various patterns. For this study, Shelford used a large number of taxa, from around the world. However, no evidence, other than its simplicity, is given to support the assertion that the 28-spotted elytron represents the primitive, ancestral condition, and thus tthis conclusion is largely suspect. Shelford also experimentally modified temperature and humidity during larval development, and found that warm conditions resulted in reduced light markings. From geographic data for a few North American species he concluded that bright colours were more common in arid areas, reduced light markings in warm areas, and expanded light markings in cool areas. These generalizations, however, were weakly corroborated, and have not been upheld by subsequent research, including the research presented here. The idea that many tiger beetles have evolved colouration to match their usual substrates was suggested by Townsend (1886). Since these early works, tiger beetle colouration patterns have been interpreted in terms of substrate matching and crypsis (Schultz, 1986; Willis, 1967), mimicry (Acorn, in press; Chapter III), thermoregulation (Chapter IV), intraspecific signalling (Pearson, 1988), and as aposematic warning colours (Pearson, 1985).

Historical biogeographic hypotheses have been constructed for the littoral tiger beetles of the Great Basin (Wickham, 1904), and for a number of species in the American southwest (Rumpp, 1961). Similar analyses have been advanced to explain the distribution of the sand dune tiger beetles *C. formosa* Say (Gaumer, 1977), *C. hirticollis* Say (Graves *et. al.*, in press), *C. longilabris* Say (Spanton, in press), *C. limbata*, and *C. duodecimguttata* (Freitag, 1965).

Here, I bring together the results of my own work on the function of tiger beetle colouration and the distribution of dune tiger beetles in the Canadian prairies with that of other authors on the systematics and distribution of dune tiger beetles in general, to produce an hypothesis regarding the history of dune tiger beetles in the Canadian prairies.

METHODS

Distribution records, taxonomy, and dune field names

Tiger beetle specimens were collected from upland dune areas in Alberta, Saskatchewan and Manitoba, as well as dune sands in the southwestern Yukon Territory. These collections plus records from the University of Alberta Strickland Museum, the J. L. and B. F. Carr collection (Calgary, Alberta), and the publications of Boyd *et. al.* (1982), Gaumer (1977), Graves *et. al.* (in press), Hilchie (1985), Hooper (1969), Larson (1986), and Wallis (1961) were used to estimate the distributions of dune tiger beetle species.

Standard names are not available for all dune areas, so the names used in this paper are presented here, and on Figure V-1. The Empress Dunes are situated 11 km. south of Empress, Alberta, along the Alberta-Saskatchewan border (see Chapter II for description of this area). The actively moving portion of the Burstall Dunes is located six km north of Burstall Saskatchewan, and is separated by cropland from the Empress Dunes and the Great Sand Hills of Saskatchewan. The latter is a huge sand dune area in southeastern Saskatchewan, with its center about 30 km east of Fox Valley. The Manitoba sand dunes are located in Spruce Woods Provincial Park, Manitoba. Various names are available for this dune field: the Aweme Dunes, the Spruce Woods Park Dunes, the Carberry Dunes, the Bald Hills, the Glenboro Dunes, the Manitoba Dessert, the Punch Bowl (refers to one blowout within the dune field), and the Spirit Sand Hills. Since this is the only large active dune field in Manitoba, I refer to it simply as the Manitoba Dunes. This is the area where Criddle (1907, 1910) made his pioneering observations on *Cicindela* behaviour.

The Gem sand dunes are almost entirely stabilized, and cover a large area between the town of Gem, Alberta, and Highway 36, south of the Red Deer River. The Hilda sand dunes are also stabilized, and are centered about five km northwest of the town of Hilda along Highway 41. The Middle Sand Hills are largely contained within the northeast corner of the Suffield Military Reserve in southeastern Alberta, but some stabilized dunes can be found just north of the reserve. The largest dune field of all is the Lake Athabasca Sand Dunes, primarily situated south of Lake Athabasca in Saskatchewan, and including a small dune field nearby in northern Alberta.

Most geographically distinctive colour morphs of dune *Cicindela* have at one time been given subspecific names, although some of these taxa have subsequently been synonymized in order to minimize the number of named subspecific taxa in the light of widespread clinal variation. Here, for ease of discussion, I have used available names for distinctive populations. I argue below that the geographic pattern of variation in these beetles in largely a function of relatively frequent changes in the extent of available habitats, and that intraspecific variation can change from discrete to clinal, or *vice versa*, relatively quickly, making formerly discrete subspecies into broad geographic clines, or alternately extirpating intergrade populations and producing distinctive populations in surviving refugia. The potentially controversial subspecies names I use here are *C. scutellaris criddlei* Casey (synonymized with *C. s. lecontei* Haldeman by Wallis [1961]), *C. formosa manitoba* Leng (synonymized with *C. f. generosa* Dejean by Gaumer [1977]), and *C. tranquebarica borealis* Harris (not recognized as valid by Wallis [1961]).

Assumptions in historical biogeography

Historical biogeographic hypotheses consist of internally consistent arguments incorporating information from palaeontology, phylogeny reconstruction, palaeogeography, as well as vagility, present geographic ranges and ecological associations. These arguments attempt to trace the evolution and past geographic ranges of lineages of organisms.

Species level phylogenetic information is of little help in elucidating Quaternary biogeographic events involving beetles, since most Pleistocene coleopteran fossils are readily assignable to extant species, although subspecific divergence without full speciation may have been common (Coope, 1970). Many tiger beetle subspecies appear to have evolved since the Wisconsin period (Gaumer, 1977; Graves *et. al.*, in press). Thus, by elucidating the plesiotypic colour pattern among subspecies it may be possible to identify more recently derived lineages.

In general, it appears that beetles have not behaviourally or physiologically changed their habitat associations over time (Coope, 1970), and thus I assume here that the palaeogeography of aeolian sand areas was correlated with the palaeodistribution of dune tiger beetles. Tiger beetles associated with open sand show evidence that the physical characteristics of the habitats, and not particular species of plants, are the determinants of habitat associations (Chapter II). Thus, the palaeodistribution of plants is less important than the palaeodistribution of dunes in elucidating past geographic ranges of tiger beetles. The northern limits of the distributions of some species may be determined by climate, and there is evidence that overwintering mortality limits the geographic ranges of *C. formosa* and *C. scutellaris* (Chapter II).

I have never seen evidence of long distance flight by dune tiger beetles, and I assume here that long distance dispersal is uncommon. Flight in tiger beetles is usually restricted to short flights for convective cooling (Morgan, 1985) or escape from predators. The presence of distinct subspecies in close geographic proximity (eg. *C. f. formosa* in the Empress Dunes and *C. f. gibsoni* in the Great Sand Hills of Saskatchewan) supports the proposition that the vagility of these tiger beetles is very low indeed. *Cicindela limbata* may be more vagile than the other species treated here, and this is discussed below.

In elucidating glacial refugia it is common practice to assume that an organism spent the Wisconsin period in a refugium which is included in the organism's present range (eg. Larson, 1975). The same logic can be applied to very large dune fields, which can be thought of as refugia during periods when small sand areas were likely to have been stabilized by plants. The presence of subspecies endemic to the area in and around these large dune fields suggests that this is a reasonable assumption.

QUATERNARY CHANGES IN DUNE GEOGRAPHY

Dunes and climatic change

The formation of active dunes requires a geological source of sand (any patch of open sand greater than four to six meters long) which has been exposed to strong prevailing winds (Bagnold, 1941). A moving dune will then remain active unless it is stabilized by plants, or is otherwise depleted of loose, open sand. Drought conditions discourage the growth of most species of prairie plants, and thus periods of arid climate encourage dune formation (Ahlbrandt *et. al.*, 1983).

Four general periods of aeolian activity have been postulated, based on sedimentological evidence and radiocarbon dating of archaeological and palaeontological materials, for the large dune fields of Wyoming, Colorado, South Dakota, Nebraska, and Kansas, which lie outside the maximum extent of Wisconsin ice (Ahlbrandt *et. al.*, 1983). The first phase occurred in the early Holocene, shortly after glacial retreat. The second phase occurred during the mid Holocene, in the warm, dry Hypsithermal period. The third phase occurred about midway between the Hypsithermal and present time. The fourth phase is essentially recent, during the last 500 to 800 years, during which "drought conditions persisted long enough in parts of the Sand Hills that vegetation was reduced enough for eolian activity to occur a number of times" (Ahlbrandt *et. al.*, 1983). No evidence was found that these dunes were first formed in the Pleistocene. Essentially, these authors postulate numerous, relatively rapid onsets of dune movement during arid periods of the Holocene. These periods of aeolian activity do not appear to have been precisely simultaneous in all dune fields.

A similar pattern of dune chronology may apply to western Canada. The Holocene climatological history of western Canada has been the subject of numerous studies, but none of these have dealt specifically with dune fields. In general, evidence indicates a warming trend following deglaciation, which peaked in the arid Hypsithermal period before cooling toward its present state (Budyko, 1982). The Hypsithermal was presumably associated with increased aeolian activity, and actively blowing dunes on most large sand deposits. The arctic plains may have been a vast sand desert during this period (Raup and Argus, 1982). Since the Hypsithermal, there has been a period of moderate warming from 800-1100 A.D. (the little climatic optimum), and a cooler period (the little ice age) during the 1700's and 1800's. The most recent significant climatic fluctuation was the warm, dry Dust Bowl period of the 1920's and 1930's.

Most of the smaller dune fields in western Canada seem to have decreased in size since the 1930's. Air photos dating back to 1938 show decrease in active sand in the Empress dune field, which will probably be completely stabilized within the next two decades if the present rate of stabilization persists unchanged. The area of open sand in the Empress dunes was approximately 48 ha in 1938, 29 ha in 1951, 13 ha in 1962, and 5 ha in 1984. Air photos, from the same years, of the Gem sand dunes and the Middle Sand Hills also show much greater areas of open sand in 1938, which have become progressively stabilized to the present. Poor air photo coverage, and the presence of numerous small blowouts rather than large dunes unfortunately made it impossible to accurately measure the area of open sand on the latter two dune fields through time. Land owners in the Middle Sand Hills of Alberta (within and north of the Suffield Military Reserve) and the Burstall Dunes, and park employees in the Manitoba dunes all report that the amount of open sand in these dune fields is rapidly decreasing. Although the 1980's have included numerous periods of drought from the point of view of agriculture, but so far I have seen no evidence that lack of moisture is sufficient to cause increase in the area of open dsand on any of the dunefields I have visited.

Bark (1978) summarizes evidence that severe droughts have been a frequent occurrence on the Great Plains in the last few hundred years, the longest of which (based on tree ring studies) lasted 38 years. These droughts presumably caused tremendous fluctuations in the size of available open sand habitats in the Great Plains.

Very large dune fields may not disappear entirely during periods amenable to plant growth, since stabilization generally proceeds from the edges of an active sand area toward its center; the larger a continuous dune area the longer it takes to stabilize. There are no indications that the Lake Athabasca Dunes are decreasing in size, and active dunes have probably existed in this dune field for 9000 years or more (Raup and Argus, 1982). The three very large dune fields in western Canada (the Lake Athabasca Dunes, The Great Sand Hills of Saskatchewan, and the Manitoba Dunes) are likely to have remained active, at least in part, throughout the Holocene. Smaller dune fields, and blowouts in sandy areas, probably appeared and disappeared with climatic changes, as they seem to have done recently.

Dune formation and disturbance by ungulates and humans

Many open sand areas have been created by human disturbance, primarily through road construction and sand excavation, and now have tiger beetle populations. In western Canada, only a small proportion of the tiger beetle localities I have seen are natural dunes or blowouts. I give evidence below that these new habitats have been important for the dispersal of *Cicindela limbata*, and possibly other species.

Another potential source of dune formation is fire, but many species of plants are adapted to colonize areas in the wake of fire, and thus if conditions are suitable for their growth they will rapidly stabilize burned-over areas. In the boreal forest, most sand dune areas are now covered by jack pine, which relies on fires for reproduction, and is thus adapted to stabilize dunes over many generations. In the grasslands, fires on dune areas in the past decade have not resulted in new dune formation (personal observation, and conversation with land owners). However, on the periphery of the Lake Athabasca dunes, Raup and Argus (1982) suggest that numerous blowouts have been initiated by fires in the pine forests, although evidence is not provided. It is possible, however, that fires in pine forests may have graeater potential to expose sand to wind action because of the greater fuel present in forests as compared to grasslands (A. W. Bailey, pers. comm.).

Animal disturbance, especially in times of drought, has also been implicated in the formation of dunes in the Great Sand Hills of Saskatchewan (Hulett *et. al.*, 1966). Although the vegetation of dune fields is notoriously poor forage for ungulates, and cattle clearly avoid sand dune plants when given the opportunity to forage on nearby grasslands (personal observation), it is possible that localized overgrazing may have caused dune formation in some areas, particularly during the first half of this century when the effects of overgrazing were less widely understood.

Male bison, during the spring breeding season, create wallows (oval depressions in which the vegetation is trampled and open soil is exposed) which could conceivably lead to dune formation in sandy areas, although in grasslands, soil compaction promotes water retention in wallows, and distinctive vegetation types (Polley and Collins, 1984). As well, free ranging bison may have choosen muddy or dusty spots for wallows, and not sand (Roe, 1951) Another effect of the huge bison herds, localized overgrazing, was a significant factor in determining prairie vegetation before bison numbers declined with the coming of European settlers, but historical record apparently provide no direct indications that this effect extended to include dune formation (England and DeVos, 1969).

The pattern of rapid dune stabilization since the 1930's suggests two alternative explanations. The dunes may have been actively moving for long periods of time prior to the 1930's, subsequent to which the factors maintaining open sand ceased to operate. Or, on the other hand, the large amount of open sand at the end of the 1930's may have been unusual, and the result of conditions during the 1930's. The first alternative is consitent with the proposition that supression of fires led to dune stabilization, but I argue above that fire is not of great importance in dune formation, at least in grasslands. The second alternative seems more likely, the most obvious possible causes of dune formation being drought conditions and localized overgrazing by cattle. The widespread pattern of rapid dune stabilization since the 1930's suggests that climate may be the primary cause, but overgrazing cannot be ruled out, especially since drought conditions would exacerbate the impact of localized overgazing. I conclude that prior to 1940 the extent of open dunes was unusually high, as a direct and indirect consequence of aridity during the Dust Bowl years.

In summary, open blowing sand appears and disappears with climatic change, and various forms of animal and human disturbance. The early par t of this century saw a general increase in open sand habitats, many of which have been rapidly stabilized since. Human disturbance, however, has acted to increase open sand habitats during this same time period. Thus, recent factors influencing the distributions of dune tiger beetles are complex, while climatic fluctuations in the past have likely resulted in the inception and extirpation of numerous local, more or less isolated populations of beetles on small, transient dune fields. The precise chronology of these dune-forming periods (which is probably unrecoverable) is of less consequence for the study of tiger beetles than the general proposition that small dune fields come and go while very large fields remain active.

BIOGEOGRAPHIC HYPOTHESES

The peculiar subspecific differences in tiger beetle faunas among the dune fields of the Canadian prairies cannot be readily explained in terms of differential local selection pressures on the various dunes, since selection pressures in such similar habitats in close geographic proximity are unlikely to have promoted the observed differences in colour pattern. Wickham (1904) encountered a similar pattern while studying beetles in the Great Basin of the United States, where "the distribution of certain species of Coleoptera could not be accounted for by the zonal arrangement of life, but apparently had as ultimate causes some condition or combination of conditions which belonged to the geological rather than the present history of the area under discussion."

Whereas the genus *Cicindela* is found throughout North America, dune dwelling species are almost exclusively restricted to a latitudinal range from southern Canada to the central United States. Further north, *C. formosa* , *C. scutellaris* , and *C. lepida* are absent, possibly because of intolerably cool climates and high overwintering mortality (Chapter II). Further south, conditions may be unfavourable because of higher temperatures, and the presence of sand-dwelling lizards (Stebbins, 1966), potentially important predators of tiger beetles (Pearson, 1985). In California, the only species of *Cicindela* found in active upland dune fields is *C. tranquebarica*, a habitat generalist (Andrews *et. al.*, 1979). Thus it appears that the North American dune tiger beetle fauna persists only within a,limited latitudinal range.

Historical Biogeographic Interpretations by Species

Only those species which are strongly associated with open blowing sand are treated here, since only they can be interpreted in terms of the palaeogeography of active dunes.

Cicindela limbata Say (Plate V-1: a-e, Map Fig. V-2):

This species is represented by two subspecies in Canada (*C. l. hyperborea* and *C. l. nympha*), and two in the Great Plains of the United States (*C. l. limbata* and *C. l. albissima* Rumpp). *Cicindela limbata hyperborea* lives entirely within the formerly glaciated region of northern Canada, and is the only subspecies without expanded light markings. This subspecies has not become adapted to northern conditions by increased dark markings (*contra* Rumpp, 1961) since its elytral pattern is a plesiotypic retention (Freitag, 1965). It has been suggested that *C. l hyperborea* survived glaciation north of the ice, and that the present subspecies of *C. limbata* are the result of Pleistocene vicariance of an originally widespread *C. l. hyperborea*-like population (Rumpp, 1961). However, extensive collecting in open sand habitats west of the Lake Athabasca Dunes has failed to produce any *C. limbata*, and thus it is unlikely that this subspecies survived in the Beringian refugium during the Wisconsin glaciation, despite evidence that there were widespread dune areas in Beringia during the glacial maximum (Hopkins, 1982).

Without evidence of geographic barriers to intergradation, it is difficult to imagine how four subspecies could have retained their identity throughout the glacial and interglacial periods of the Pleistocene, and it must therefore be considered that these taxa may have evolved since the melt of the Wisconsin glaciers. The alternative, that each subspecies was confined to a different refugium and then dispersed to previously glaciated areas without intergrading with other subspecies, possibly numerous times throughout the Pleistocene, seems unlikely.

The subspecies *C. l. albissima* is endemic to the Coral Pink Sand Dunes of Utah, an area with an endemic plant species as well (Bowers, 1984). This is the only population of *C. limbata* west of the continental divide (presumably because the mountains form an effective barrier to dispersal), and has presumably evolved in isolation *in situ* (Rumpp, 1961). The Coral Pink dunes may have been habitable throughout the Holocene (Bowers, 1984), and thus this subspecies could have evolved within the last 10,000 years.

Cicindela limbata nympha, in the northern Great Plains, and *C. l. limbata*, in the southern Great Plains differ with respect to ground colour; brown in the former and green in the latter. Ground colour differences in *C. circumpicta* LaFerté affect susceptibility to predation by kestrils (Willis, 1967), and selection for crypsis may have resulted in geographic differences in ground colour between the subspecies of *C. limbata* as well. Although *C. l. nympha* is widespread today, almost all collecting localities are areas of human disturbance in sandy areas. The only natural habitats available for these beetles are the dune fields of the prairies, and I argue that this subspecies would be restricted to these dune fields if not for the activities of people. In northern Saskatchewan there is an area of intergradation between *C. l. nympha* and *C. l. hyperborea*, subspecies previously thought to be disjunct (Wallis, 1961). Specimens in this area have been collected only recently, since roads were not present earlier, and all collecting localities are sandy roadcuts associated with the new highways. I argue, therefore, that *C. l. nympha* and *C. l. hyperborea* have been largely restricted to prairie and northern dune fields until quite recently when new habitat was created during the Dust Bowl era and by subsequent human disturbance. The vagility of this species seems to be greater than that of other dune *Cicindela* in Canada, and is clearly demonstrated by the rapid colonization of isolated new patches of open sand in Alberta, at Gull Lake (beach dunes formed in 1971 and were colonized within two years-- the population is now extirpated, and the dunes are stabilized), Bindloss (a roadcut made in 1983), and Winterburn (sand pit excavations in dunes previously covered with parkland forests). The presence of *C. l. hyperborea* near Goose Bay, Newfoundland also suggests a recent colonization event (Larson, 1986). Thus, discontinuities in the range of this species are, or have been, the result of lack of habitat, not low vagility.

Increased aridity following deglaciation presumably created numerous areas of suitable habitat for *C. limbata* between the major dune fields, and a broad zone of intergradation such as now exists in northern Saskatchewan. Subsequent climatic cooling would extirpate these intergrade populations, however, giving the impression of long-term isolation between the subspecies. Thus, because of the probability of such reticulate phylogenies, these subspecies cannot be analyzed using the assumptions of vicariance biogeography, even when an apparent vicariant distribution pattern is seen.

C. hirticollis **Say (Plate. V-1: f-g, Map Fig. V-3):**

This species is represented by two subspecies in Canada, and only these will be treated here. *C. hirticollis* is found throughout the prairies on open, dry sand near water, and presumably has been able to follow river valleys in dispersal, living on sand bars (Graves *et. al.*, in press). These populations have complete elytral markings and brownish ground colour. Wallis refers to these beetles as *C. h. ponderosa* Thomson, but Graves (in press) has shown that this subspecies is restricted to its type locality (Veracruz, Mexico) and thus proposed a new name (as yet unpublished) for the prairie populations.

Graves (in press) has also named another subspecies, which is restricted to the Lake Athabasca Dunes, and presumably evolved *in situ* during the Holocene. These beetles have reduced light elytral markings, and brown, green, or blue-green ground colour. I have seen one blue specimen of *C. hirticollis* from Jasper Lake, and a series of greenish specimens without reduced markings from Lesser Slave Lake. These three sites are connected by the Athabasca River drainage, and may represent intergradation between the two subspecies. However, green colour may also be the result of physical conditions at the periphery of the species' range, and may be environmentally induced and not indicate relatedness. Populations of *C. longilabris* at high altitudes also show green colour (Spanton, in press). This problem is discussed further below.

In general, it would seem that an isolated population of *C. hirticollis* has evolved distinctive characteristics in the Lake Athabasca dunes, presumably during the Holocene. The alternative, that this distinctive population dispersed to the Lake Athabasca dunes from a distant refugium without intergrading with the widespread prairie form, is much less likely.

Cicindela scutellaris **Say** (Plate. V-1: h-j, Map Fig. V-4):

This species has six subspecies, of which three are found in western Canada. *Cicindela scutellaris scutellaris* is found in southern Alberta and Saskatchewan, and has no light markings on the elytra. The colouration of this subspecies mimics that of the sympatric meloid beetle *Lytta nuttalli* Say (Acorn, in press; Chapter III). The subspecies, *C. s. lecontei* Haldeman, is found in much of southeastern Canada and the eastern United States, and has the light elytral markings reduced to small triangles on the elytral margin, corresponding in position to the bases of the humeral and apical lunules and the middle band. In and around the Manitoba dunes, however, populations with the light markings expanded along the margin are found, and have been given the name *C. s. criddlei* Casey. This light elytral pattern is not the typical thickening of the plesiomorphic complete pattern (seen, for example, in *C. limbata nympha* and *C. formosa gibsoni*), but expansion of the derived markings seen in *C. s. lecontei*, suggesting that Holocene isolation in the Manitoba dunes of a population similar to modern *C. s. lecontei* gave rise to *C. s. criddlei*.

C. formosa Say (Plate. V-1: k-o, Map Fig. V-5):

Two Canadian subspecies of *C. formosa* have their ranges centered on large dune fields, while another two are widespread in sand habitats east of the Rocky Mountains. *Cicindela formosa gibsoni* is found only in and around the Great Sand Hills of Saskatchewan, and has presumably evolved from a population resembling present day *C. f. formosa* in this area since the last glaciation (Gaumer, 1977). Members of the Empress population, which Wallis (1961) and Hilchie (1985) refer to as *C. f. formosa*, have more expanded light elytral markings than typical *C. f. formosa* and are likely intergrades between *C. f. formosa* and *C. f. gibsoni*. Gaumer (1977) states that *C. f. formosa* have between 30 to 40% (rarely over 45%) of the elytra covered by light maculations, while *C. f. gibsoni* have 65-95% of the elytra white. A sample of 77 *C. formosa* from Empress ranged from 40 to 65% light elytral area, with a mean of 48.8% (using Gaumer's illustrations as a guide to determining percent light area for each specimen). This is consistent with the proposition that the Empress dunes became active during the Dust Bowl and have been colonized since, primarily by *C. f. formosa* from the south and secondarily by *C. f. gibsoni* from the east. This population will soon be extirpated, as the Empress dunes become stabilized and habitat for the beetles consequently disappears. Thus, clinal variation today may become disjunct in the foreseeable future. The pattern of expansion and contraction of available habitat around large dune fields might explain the observation that many subspecies of tiger beetles have their ranges centered on major dune fields, although they may intergrade with other subspecies on the periphery of their ranges.

Similarly, in the Manitoba Dunes, *C. f. manitoba* may have evolved from a population resembling modern *C. f. generosa* . A north-south cline connects these forms, leading Gaumer (1977) to synonymize the names, referring to both forms as *C. f. generosa*. It is likely that *C. f. manitoba* evolved expanded light elytral markings *in situ* in the Manitoba Dunes, subject to similar selection pressures as the populations of *C. f. gibsoni* in the Great Sand Hills of Saskatchewan.

In the Yampa Valley of Colorado, another isolated population of *C. formosa* has evolved expanded markings. This population was originally referred to as *C. f. gibsoni*, but Gaumer (1977) has demonstrated that differences in larval structure suggest convergent evolution of expanded markings in adults of these two forms. Thus, at least for these subspecies, isolation in a single dune field has resulted in light colour, while inhabitants of small sand areas without dunes have retained the complete elytral pattern. In Canada, many apparently suitable small sand areas have no *C. formosa* populations (Wallis, 1961), further supporting the contention that populations at this latitude could be easily isolated in large dune fields. Gaumer has suggested that well-drained sand is essential to this species, which may explain its virtual absence from the Burstall dunes and the northern portion of the Great Sand Hills of Saskatchewan, south of Sceptre, both of which support the growth of willow and poplar trees (Chapter II).

***Cicindela lengi* W. Horn** (Plate V-1: p-q, Map Fig. V-6):

All Canadian populations of this species have been called *C. l. versuta* Casey, despite some obvious variations in ground colour, which may indicate selection for substrate matching. Northern populations, from the Yukon and northern Saskatchewan, have much darker ground colour than those further south (based on specimens from the J.L. and B. F. Carr collection in Calgary), but there is no indication that these beetles live on darker soils. Populations in Alberta and Saskatchewan have reddish ground colour, while those in Manitoba are more brownish. This red-brown colour difference is also seen between *C. f. formosa* and *C. f. generosa*, and may be evidence of selection for substrate matching. Shultz (in litt.) suggests that *C. formosa formosa* may have evolved cryptic reddish colouration on red bed soils, and this explanation may apply to western *C. lengi* as well.

***Cicindela lepida* Dejean** (Plate V-1: r, Map Fig. V-7):

This species is monotypic throughout its range, and is restricted to dune sands in the prairies. It does, however, show some evidence of relatively recent range extension. Wallis (1961) does not list this species from the Empress dunes, although he does list other summer *Cicindela* such as *C. punctulata* and *C. pusilla*. It is therefore possible that *C. lepida* had not yet dispersed to the Empress Dunes; further evidence that the dune field became active in the Dust Bowl and was then colonized by tiger beetles.

THE EVOLUTION OF ELYTRAL PATTERN IN *CICINDELA*

The primitive elytral pattern

No phylogenetic reconstruction has been attempted for the tiger beetles as a whole, but the species of *Cicindela* have been grouped into numerous subgenera by Rivalier (1950, 1954, 1957, 1961, 1963). These non-phylogenetic attempts to group species on the basis of structural similarity among adults may contain nearest relatives, but the similarities might also be the result of convergent or parallel evolution. Phylogenetic reconstructions are available for some groups within the subgenus *Cicindela*, notably the *C. maritima* group (Freitag, 1965, 1972; Rumpp, 1967), the subspecies of *C. formosa* Say (Gaumer, 1977), and the *C. sylvatica* group (Spanton, in press).

The complete elytral pattern, with humeral and apical lunules and a middle band (eg. Plate V-1: a, V-1: e, V-1: f, V-1: k), is widespread in the subgenus *Cicindela* and may represent the ancestral elytral pattern for this subgenus, if not the genus as a whole. The *C. maritima* group, many members of which are dune inhabitants, evolved from an ancestor which resembled *C. repanda* Dejean, with a complete elytral pattern (Freitag, 1967, 1977). The subspecies of *C. formosa* also evolved from an ancestor with a complete elytral pattern (Gaumer, 1977), as did the members of the *C. sylvatica* group (Spanton, in press). The only dune tiger beetle in Canada which is not a member of the subgenus *Cicindela* is *C. lepida*, in the subgenus *Ellipsoptera*. Adult *C. lepida* show the complete elytral pattern clearly, although the light markings are extremely broad, and the darker background colour is quite a light bronze-brown. Thus, as a working hypothesis I assume that the non dune-dwelling ancestors of the sand dune tiger beetles of the Canadian prairies possessed the complete elytral pattern.

Correlations Between Elytral Patterns and Geography

Associations among elytral pattern, habitat, and geographic ranges suggest three possible correlations: 1) only taxa found on open dunes show expanded light markings, although these beetles may be found on non-dune sand elsewhere, 2) of these beetles, only those found on upland dunes, as opposed to littoral dunes, show expanded light markings, and 3) only those found south of the boreal forest show expanded light markings.

All three correlations are consistent with the proposition that expanded light markings are a thermoregulatory adaptation since lack of shade, dry substrates, and low latitudes all are associated with higher surface temperatures. For the *C. maritima* group, these generalizations are consistent with Freitag's (1972) phylogeny (Figure V-8). Expanded light elytral markings are probably a thermoregulatory adaptation, but may also be the result of selection for substrate matching and crypsis. Expanded light markings reduce overheating at high ambient temperatures on upland dune sites with little shade, and no moist substrates (Chapter IV). Light, dry substrates and high temperatures often occur together, as on upland dunes and saline flats, and many tiger beetles in both habitats are light in colour (see Willis [1967] re. beetles in saline habitats).

Of the dune tiger beetles without expanded light elytral markings (i.e. possessing complete markings), *C. limbata hyperborea* is found only in the boreal forest region, while the plains subspecies of *C. hirticollis* is only found on sand near water. The other two (*C. formosa formosa* and *C. lengi versuta*) are found on open sand without dunes as well as in dune habitats.

I argue here that isolation in a single active dune field is correlated with expanded markings, and that *C. f. formosa* and *C. l. versuta* have not been isolated in this way. Many tiger beetle taxa are more-or-less endemic to the area in and around one major dune field. The only endemic species is *C. theatina*, which lives on the Great Sand Dunes of Colorado (and has expanded light markings). On the Lake Athabasca dunes the endemic subspecies of *C. hirticollis* has reduced markings. Further south, *C. formosa gibsoni* (endemic to the Great Sand Hills of Saskatchewan), *C. formosa manitoba*, and *C. scutellaris criddlei* (both endemic to the area around the Manitoba Sand dunes).all have expanded light markings. *C. limbata albissima* has the most expanded light markings of all the *C. limbata* subspecies, and is endemic to the Coral Pink Sand Dunes of Utah. *C. formosa* is represented by an endemic subspecies in the Yampa Valley of Colorado. Gaumer (1977) showed that this population is convergent with *C. f. gibsoni*, and named it (unfortunately a *nomen nudum* since names published only in theses are not recognized by the International Code of Zoological Nomenclature).

Reduced light markings are seen in five sand dune tiger beetles in western Canada, none of which are found on open, southern dune fields except the iridescent green and red *C. s. scutellaris* which mimics a sympatric meloid beetle (Chapter III). *C. hirticollis* from Lake Athabasca have reduced light markings and this form is endemic to the Lake Athabasca Sand Dunes of northern Alberta and Saskatchewan. The elytral pattern of this subspecies may allow it to warm more efficiently at high latitudes at cool temperatures. The reduced markings of the northern subspecies *C. tranquebarrica borealis* may also function in thermoregulation. Adult *C. longilabris* live in sandy areas with Jack Pine (a tree which requires fires to reproduce) and may mimic pieces of charred wood on the dune sands, just as *C. formosa pigmentosignata* W. Horn mimic beetle-sized fragments of purplish sandstone in Texas (Schultz, 1986). Adult *C. duodecimguttata* are found both on upland sand, where they are uncommon, and on wet sand near water where they occur in great numbers. In the latter habitat, these beetles are very difficult to see, and the hypothesis that they are cryptic on this substrate seems reasonable.

Correlations Between Elytral Ground Colour and Geography

The darker background colours of tiger beetle elytra show three interesting correlations with geography. First, many populations further north show darker colour, or greenish colour (Spanton, in press; Graves *et. al.*, in press). Second, in many instances beetles from the same area have similar colour (Willis, 1967). Third, background colour commonly matches the colour of some aspect of the substrate (Schultz, 1986).

Cicindela hirticollis from Lake Athabasca, *C. tranquebarrica borealis*, and northern populations of *C. lengi versuta* all have reduced markings as well as darker ground colour than conspecifics south of the boreal forest. Green ground colour is common in populations of *C. hirticollis* from Lake Athabasca, but its significance is difficult to elucidate. Green colour is seen in populations of *C. hirticollis* and *C. longilabris* in coastal, and (for *C. longilabris*) mountainous regions, and is clearly associated with the extremes of these species' ranges (Spanton, in press; Graves *et. al.*, in press). It is not known what factors at the periphery of the ranges might cause green colouration, if a causal relationship exists at all.

Cicindela formosa and *C. lengi* are both reddish in the Empress dunes, and both brownish in the Manitoba dunes. On the Empress and Manitoba dunes the two species are very difficult to distinguish except in the hand. These colour similarities suggest selection for substrate matching. In the Great Sand Hills of Saskatchewan, however, *C. lengi* is reddish while the ground colour of *C. f. gibsoni* is red-purple.

In the United States, Schultz (1986 and *in litt.*) has suggested that the subspecies *C. formosa pigmentosignata*, *C. f. formosa*, and an endemic subspecies named by Gaumer (1977) *C. f. mescalero* (another unfortunate *nomen nudum*) have evolved reddish ground colour to match fragments of red Permian sandstone, Permian red bed soils, and the red Mescalero sands respectively. However, there are no such red soils in the Canadian prairies, and thus the red and purple colouration of *C. f. formosa* and *C. f. gibsoni* here cannot be explained in this fashion. In the Manitoba dunes, both species are difficult to see among grasses on the brown-yellow sand, but adults of both *C. formosa* and *C. lengi* are easily seen at Empress. If, however, *C. formosa formosa* originally evolved red colour on Permian red bed soils in the western United States, this explanation could apply to *C. lengi versuta* as well, and both subspecies may retain this colour in Canada, outside the range of red soils.

AN OVERALL HISTORICAL MODEL

An overall synthesis of the factors affecting the colouration and distribution of sand dune tiger beetles in western Canada is presented in flowchart form in Figure V-10. Although largely speculative, this model is consistent with available phylogenetic and palaeogeographic information, and the observed correlations between colouration, habitat, and geographic distribution referred to above. Each of the historical biogeographic hypotheses presented above for the species of sand dune tiger beetles is consistent with this model.

Cicindela scutellaris, however, is a special case, at least in part because of the mimetic colouration of the nominate subspecies. However, the northern subspecies *C. s. lecontei* and *C. s. criddlei* can be interpreted in terms of the model, since although the elytral pattern of *C. s. lecontei* is not complete, it does become expanded in the Manitoba populations of *C. s. criddlei*.

The ancestors of the tiger beetle lineages which invaded dune habitats in western North America probably possessed the complete elytral pattern, with elytral ground colour matching some aspect of the substrate. Where these beetles dispersed to dunes in the northern boreal forest, dark or green elytral ground colour developed. On non-boreal dunes beside lakes, the complete pattern was retained without change in ground colour. On upland dune fields south of the boreal forest, the elytral markings became expanded, possibly a result of selection for thermoregulation. This general pattern was then modified by climatic change and human disturbance, which has had two general effects. Open sand habitats increased in periods of warm, dry climate, or where sandy areas were disturbed by road construction. Tiger beetles dispersed into these new habitats, and where two formerly distinct subspecies met, intergrade populations developed. Open sand habitats were restricted to large dune fields in times of cool, moist climate, in the absence of new habitat created by road construction. This resulted in the extirpation of intergrade populations and the isolation of subspecifically distinct populations on large dune fields.

From this overall model, three general conclusions can be drawn, all of which may stand as hypotheses to be tested by further work. First, climatic change has been the most important factor influencing distribution and intraspecific variation in dune tiger beetles in western Canada, acting through the creation and subsequent stabilization of open sand habitats outside the major dune fields. Second, intraspecific variation may take the form of broad geographic clines or discrete, isolated subspecies, and, over relatively short spans of geologic time these two states may alternate. Thus, any given discrete subspecies of dune tiger beetles may be a temporary or a recurrent phenomenon, or an incipient species. Third, during the time entomologists have been able to study it, the pattern of variation within dune tiger beetle species in western Canada has been changing, partly because of the effects of drought (and possibly overgrazing by cattle) during the Dust Bowl, and partly because of the effects of road construction. Thus, this system provides an exciting subject for ecological and biogeographic studies, but provides little hope that a stable subspecific nomenclature can be applied to the beetles involved.

ACKNOWLEDGEMENTS

This study has benefitted greatly from discussions with and comments from the following individuals: A. W. Bailey, G. E. Ball, J. L. and B. F. Carr, R. C. Graves, G. J. Hilchie, T. D. Schultz, C. Schweger, D. R., P. N., and K. A. Shaw, T. G. Spanton, J. R. Spence, and F. A. H. Sperling. Field assistance was provided by M. Funk, L. Shortreed, J. Spence, F. A. H. Sperling, and D. A. Wrubleski. I would like to thank J. L. and B. F. Carr for the loan of their extensive collection of *C. limbata* from northern Saskatchewan. This work was supported by a grant to myself from the Boreal Institute for Northern Studies, and by a grant to J. R. Spence from the National Science and Engineering Research Council of Canada.

Plate V-1. Dune tiger beetles: a) *Cicindela limbata hyperborea*, b) *C. l. hyperborea* X *C. l. nympha*, c) *C. l. nympha*, d) *C. l. limbata*, e) *C. l. albissima*, f) *C. hirticollis*, g) *C. hirticollis* from Lake Athabasca showing green ground colour, h) *C. scutellaris scutellaris*, i) *C. s. lecontei*, j) *C. s. criddlei*, k) *Cicindela formosa formosa*, l) *C. f. formosa* X *C. f. gibsoni* (Empress dunes), m) *C. f. gibsoni* (Great Sand Hills of Saskatchewan, east of Fox Valley), n) *C. f. manitoba* (Manitoba Sand Dunes), o) *C. f. generosa*, p) *C. lengi* (Manitoba Sand Dunes), q) *C. lengi* (Empress Sand Dunes), r) *C. lepida*. Scale bar = 1 cm.

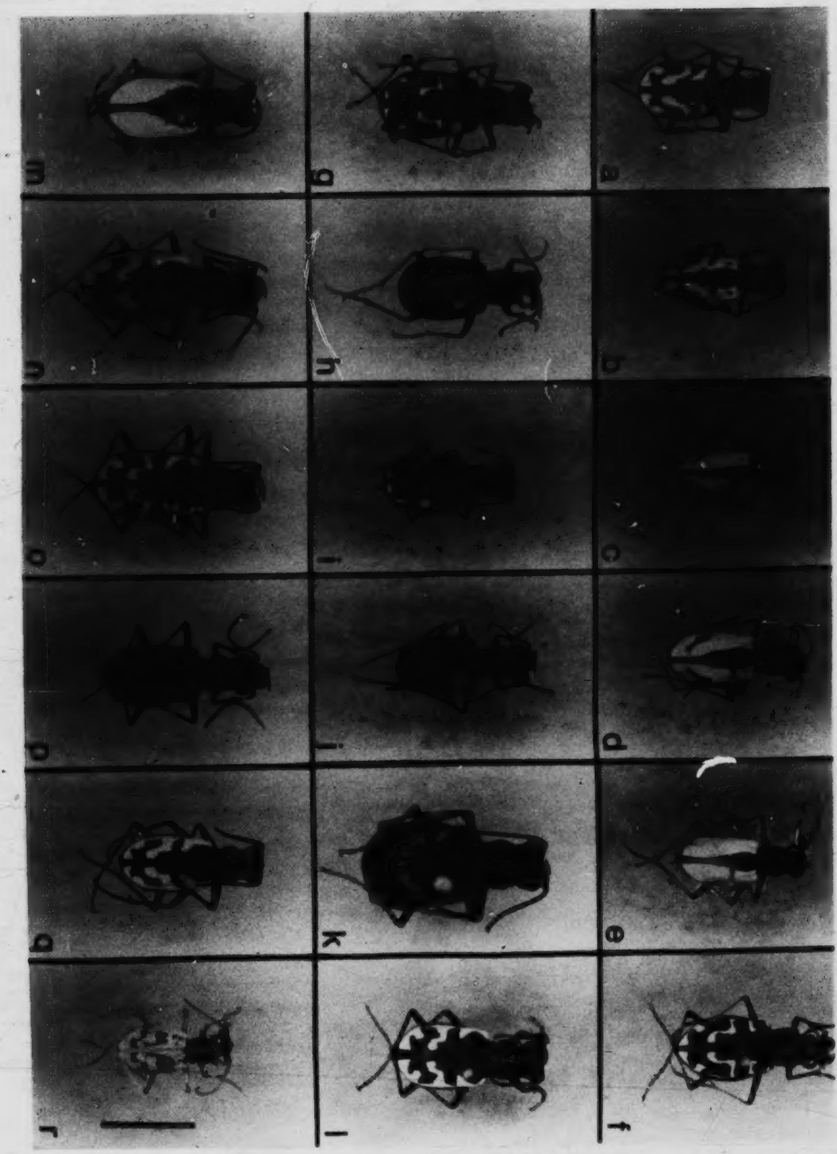
a
b
c
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Figure V-1. Map showing the locations of the western Canadian dune fields mentioned in the text.

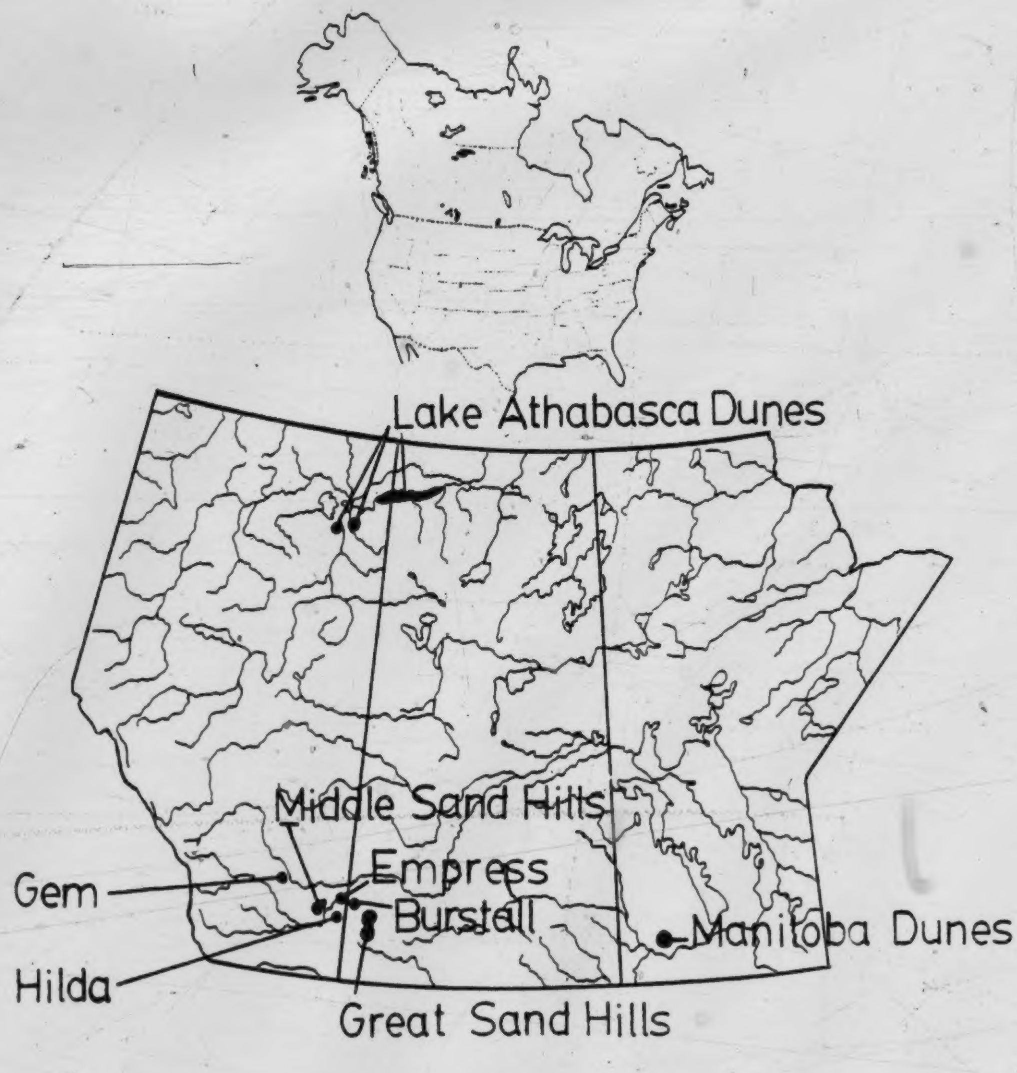

Lake Athabasca Dunes
Middle Sand Hills
Empress
Gem
Burstall
Manitoba Dunes
Hilda
Great Sand Hills

Figure V-2. Collecting localities for *Cicindela limbata* in western Canada, and approximate complete geographic range of the species. Filled circles represent localities for *C. l. nympha*, open circles represent *C. l. hyperborea*, and half-filled circles represent intergrades between the two.

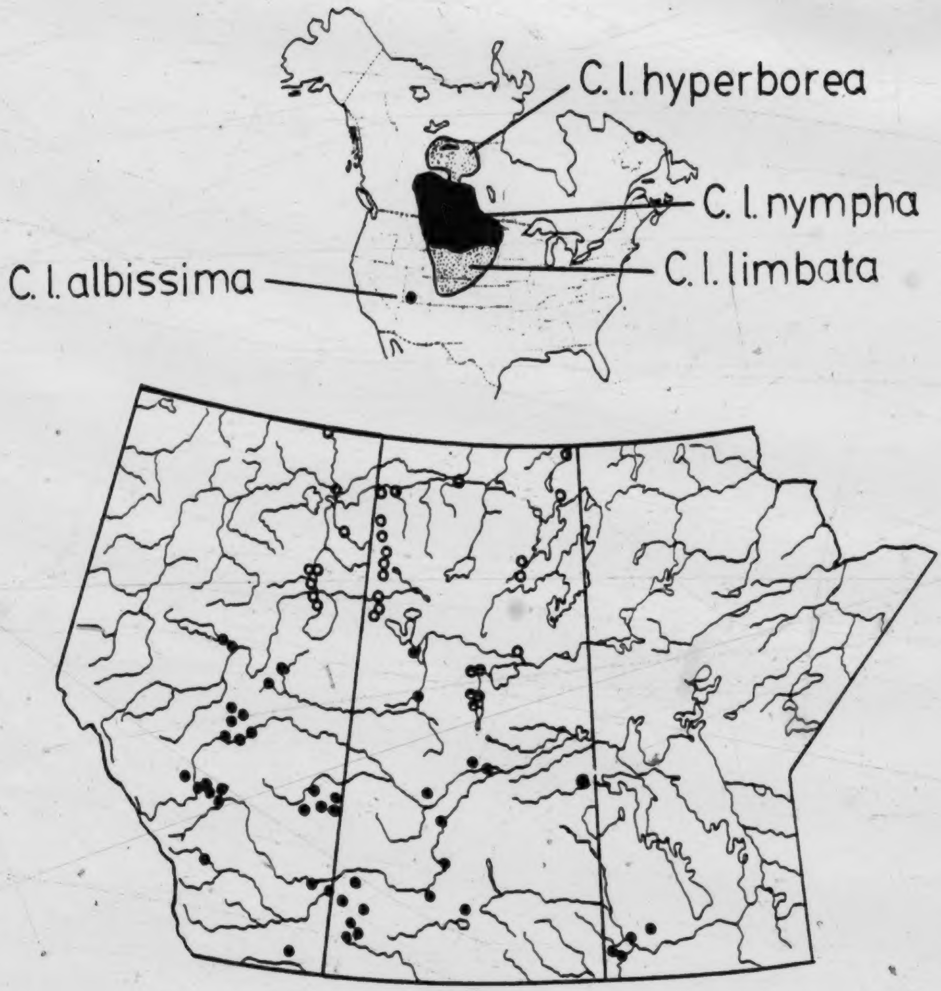

C. l. hyperborea
C. l. nympha
C. l. albissima
C. l. limbata

Figure V-3. Collecting localities for *Cicindela hirticollis* in western Canada, and approximate complete geographic range of the species, excluding the isolated population of *C. h. ponderosa* Thomson at Veracruz, Mexico. After Graves *et. al*. (in press).

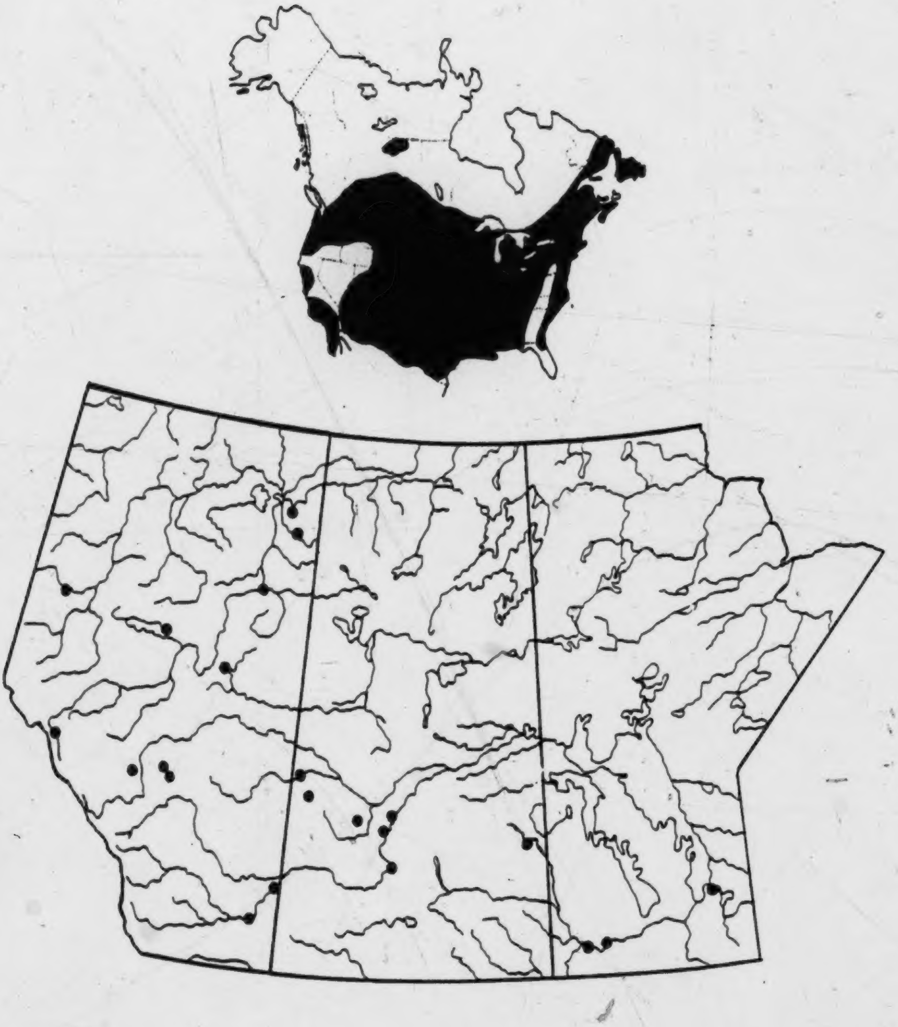


Figure V-4. Collecting localities for *Cicindela scutellaris* in western Canada, and approximate complete geographic range of the species. Filled circles represent localities for *C. s. scutellaris*, open circles represent *C. s. criddlei*.

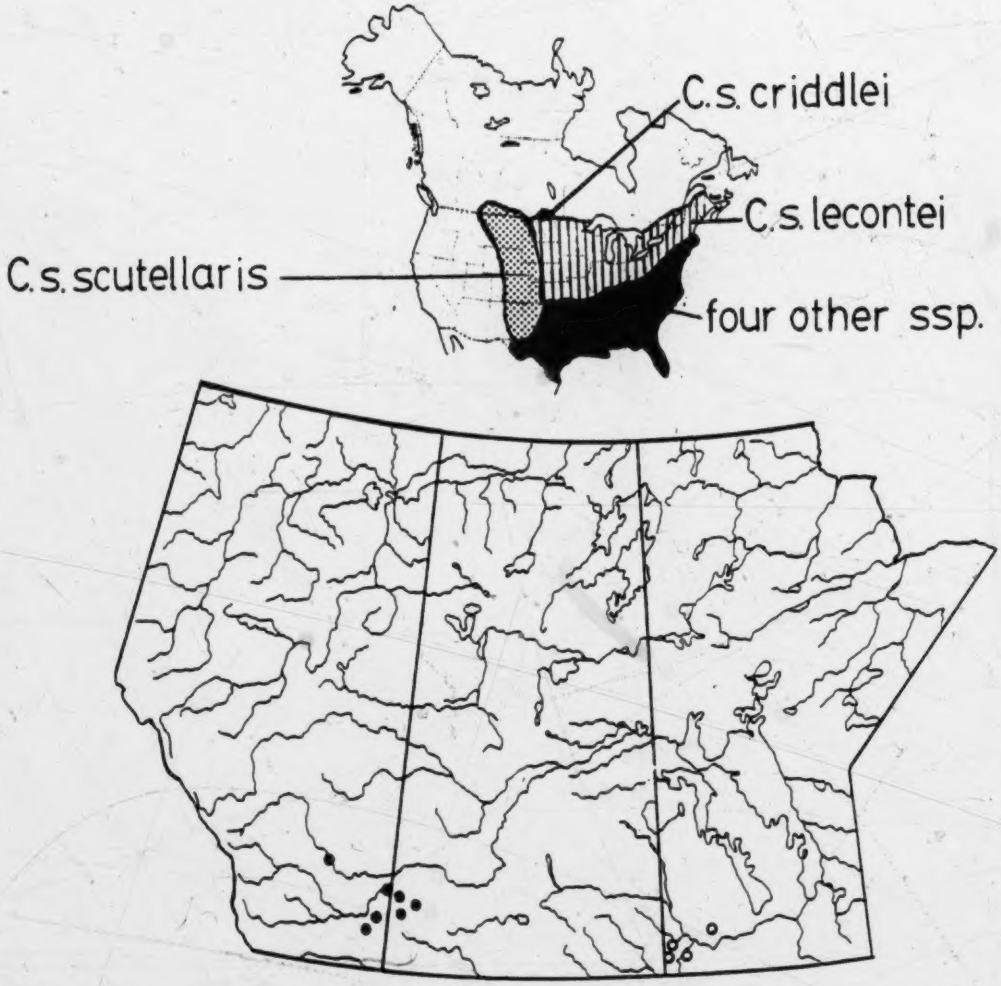

C.s. criddlei
C.s. lecontei
C.s. scutellaris
four other ssp.

Figure V-5. Collecting localities for *Cicindela formosa* in western Canada, and approximate complete geographic range of the species (after Gaumer, 1977). Filled circles represent localities for *C. f. formosa* (one, the Empress locality, is a population intermediate between *C. f. formosa* and *C. f. gibsoni*, and the other localities may be as well), open circles represent *C. f. gibsoni*, and half-filled circles represent *C. f. manitoba*.

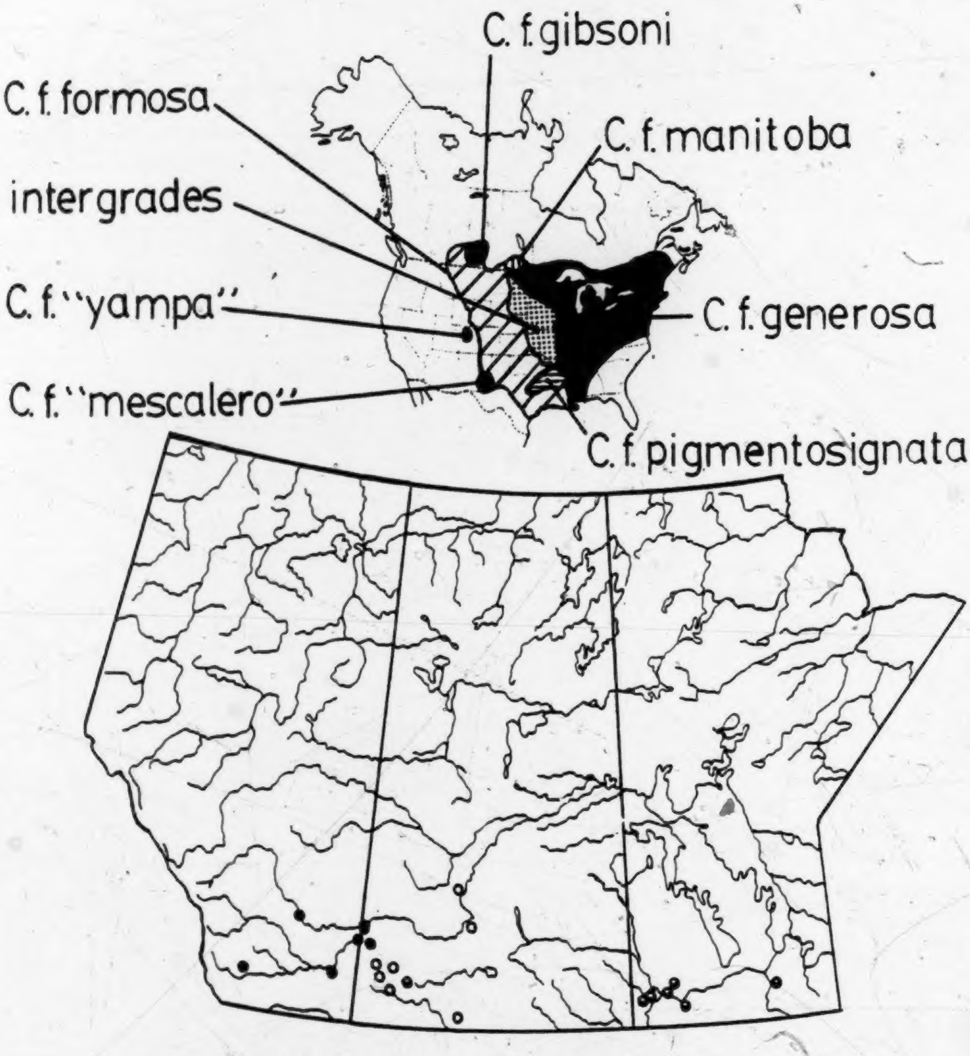

C. f. gibsoni
C. f. formosa
C. f. manitoba
intergrades
C. f. "yampa"
C. f. generosa
C. f. "mescalero"
C. f. pigmentosignata

Figure V-6. Collecting localities for *Cicindela lengi* in western Canada, and approximate complete geographic range of the species.

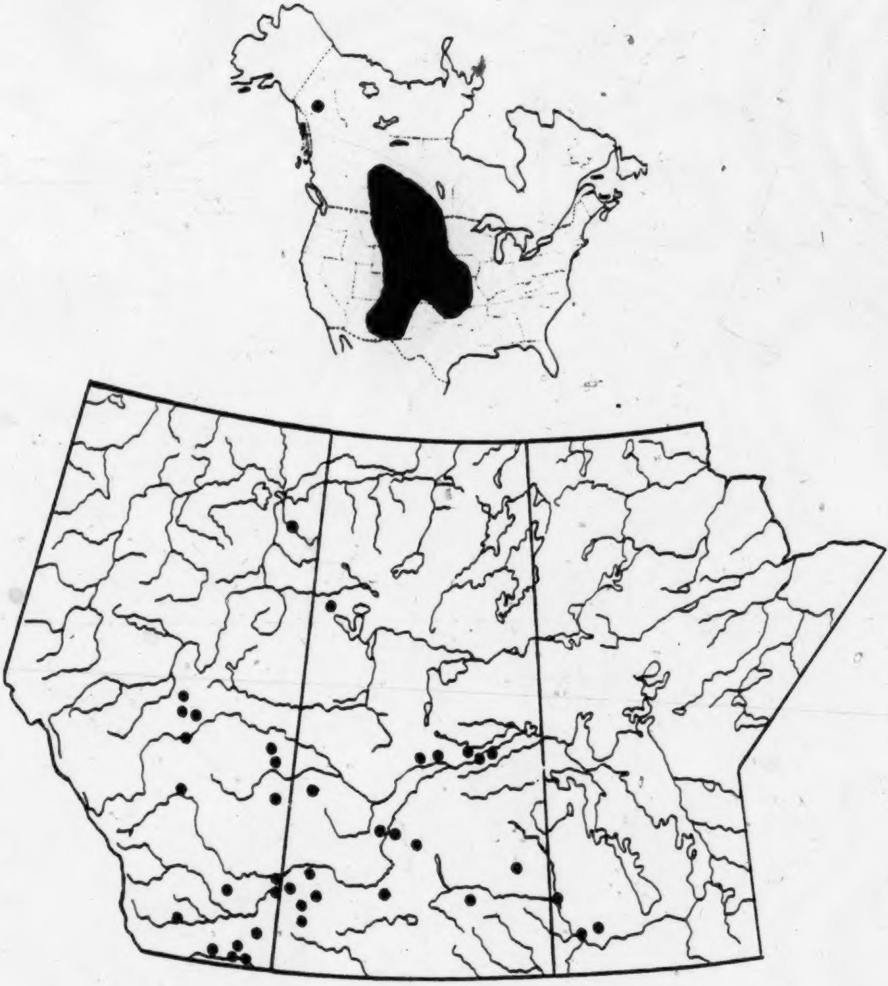


Figure V-7. Collecting localities for *Cicindela lepida* in western Canada, and approximate complete geographic range of the species.

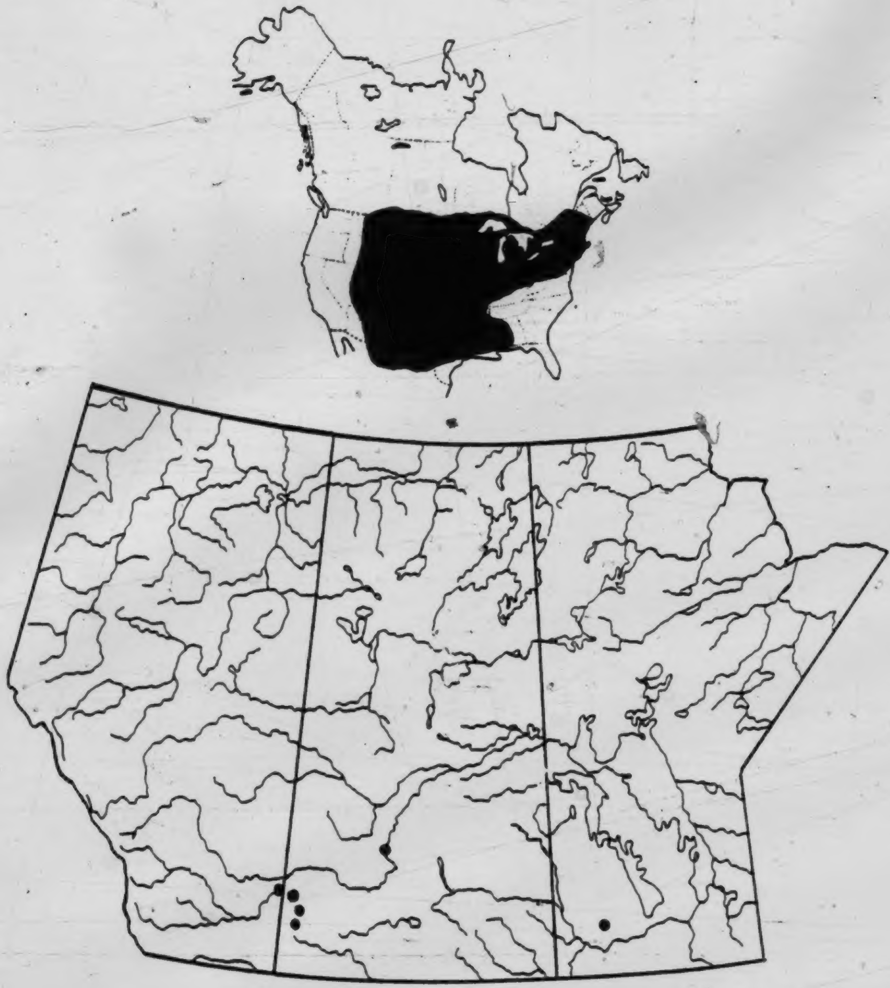


Figure V-8. Phylogeny of the *Cicindela maritima* species group (after Freitag, 1972), showing habitat associations and elytral markings. Abbreviations for habitat: R= riparian, S= sand dune. Abbreviations for elytral markings: C= complete, R= reduced light markings, E= expanded light markings.

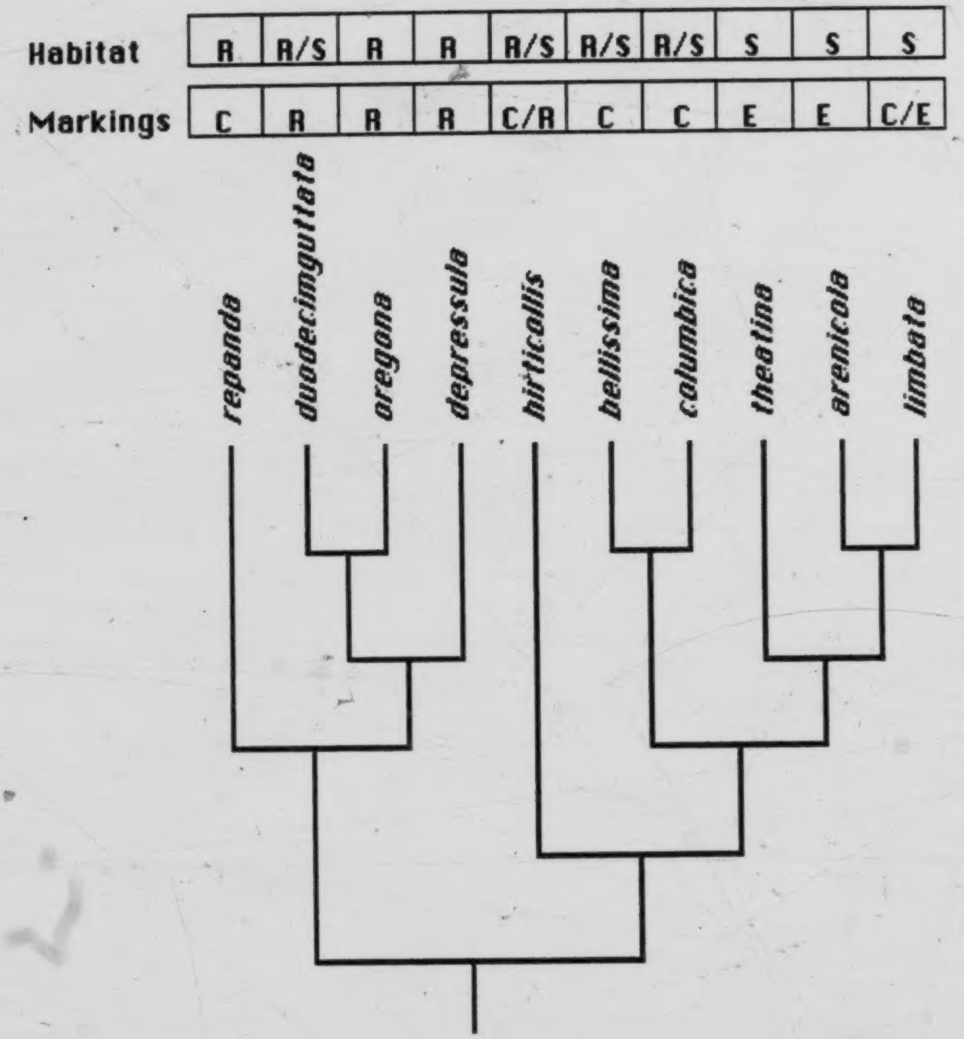
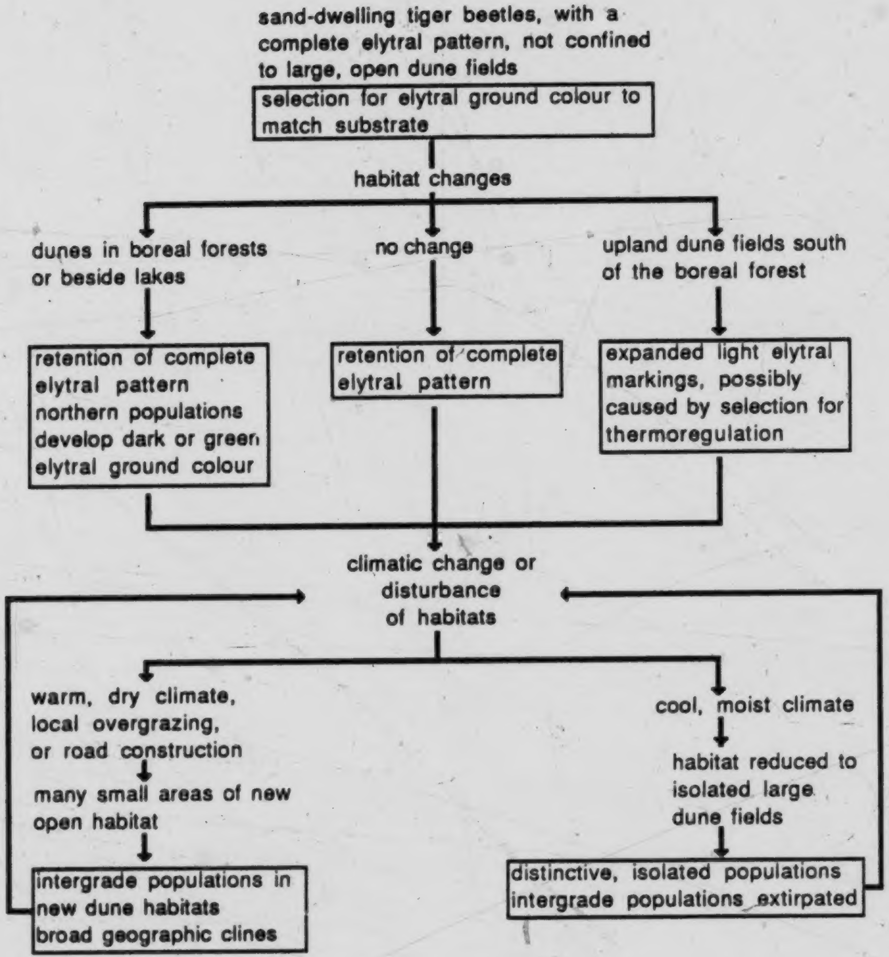

Habitat
R
R/S
R
R
R/S
R/S
R/S
S
S
S
Markings
C
R
R
R
C/R
C
C
E
E
C/E
repanda
duodecimguttata
oregona
depressula
hirticollis
bellissima
columbica
theatina
arenicola
limbata

Figure V-9. Flow chart depicting the major evolutionary and geographic factors influencing the colouration of dune tiger beetles in western Canada.


sand-dwelling tiger beetles, with a complete elytral pattern, not confined to large, open dune fields
selection for elytral ground colour to match substrate
habitat changes
dunes in boreal forests or beside lakes
no change
upland dune fields south of the boreal forest
retention of complete elytral pattern northern populations develop dark or green elytral ground colour
retention of complete elytral pattern
expanded light elytral markings, possibly caused by selection for thermoregulation
climatic change or disturbance of habitats
warm, dry climate, local overgrazing, or road construction
many small areas of new open habitat
intergrade populations in new dune habitats broad geographic clines
cool, moist climate
habitat reduced to isolated large dune fields
distinctive, isolated populations intergrade populations extirpated

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CHAPTER VI

GENERAL DISCUSSION

Because adults of most species of *Cicindela* are diurnal, generalist predators in open ground habitats, they appear to live uncomplicated lives and to have simple environmental requirements. The largest *Cicindela* adults are about five times the length of the smallest, and the typical habitus varies little within the genus, and is easily recognized among the over 100 species in North America alone.

However, less profound ecological differences among *Cicindela* species are many, and have been used to explain the mechanisms by which species can coexist in a given habitat or geographic area. Each species is exclusively associated with a particular type of soil, with a certain amount of vegetative cover, on a certain slope (see Wallis [1961] for substrate associations of the Canadian species). Life histories and phenologies differ among species, and adults of sympatric species in saline habitats show evidence of temporal segregation as well as habitat segregation (Willis, 1967).

Prey size is determined by mandible size (itself not a simple function of body size) and it has been argued that among sympatric species, resource partitioning of food items seems to have resulted in character divergence with respect to mandible size (Pearson and Mury, 1979). Thermoregulation has also been implicated in minimizing simultaneous use of limiting resources, in that thermoregulatory differences among species may facilitate coexistence by promoting temporal segregation between tiger beetles and their predators, and among tiger beetle competitors (Pearson and Lederhouse, 1987).

Variation among tiger beetle species, and among subspecies within species, is also seen with respect to colouration. White elytral markings range from thin sigmoid lines to spots, bands, lunules, or broad white patches. The ground colour of the body, including the elytra, may be black or colourful, dull or brilliant, and include any colour or colours. These colours are structural, produced by laminae in the exocuticle (Mossakowski, 1979). The significance of colouration to thermoregulation has been speculated on (Pearson and Lederhouse, 1987), but prior to my own study the relationship between the two remained largely unknown.

I have used the sand dune tiger beetles of the Canadian prairies to answer a number of questions about tiger beetle biology. First, I looked at how well the beetles on the Empress dune field conformed to the prediction of resource partitioning with respect to time, space, and food. Then, I looked at the function of colouration in these beetles. I determined that one subspecies was mimetic, and then went on to examine the thermoregulatory consequences of colouration for two other species.

With respect to patterns of distribution and abundance, the Empress *Cicindela* clearly show the effects of factors other than interspecific competition for limiting resources. Adults of one species, *C. formosa*, eat adults of two others; *C. limbata* and *C. lepida*. My data are not conclusive regarding the impact of this predation on the relative abundances of these species, but they clearly suggest that these beetles are not simply competitors. The two species which are most likely to compete for food, *C. limbata* and *C. lepida*, show no appreciable differences in mandible size or habitat association, and although they have different life history patterns both are abundant as adults simultaneously in mid summer.

Physical factors affecting thermoregulation for terrestrial animals under equilibrium conditions are summarized by the following equation (Burtt, 1981):

$$S_{abs} + T_{abs} + M - T_{rad} \pm E_{conv} \pm E_{cond} \pm E_{evap} \pm E_{st} = 0 \qquad (1)$$

where S_{abs} is absorbed solar radiation, T_{abs} is absorbed thermal radiation (long wave infrared radiation from objects in the environment), M is metabolically produced radiant energy, T_{rad} is thermal radiation from the organism, E_{conv} is energy transfer between the organism and surrounding air by convection, E_{cond} is energy transfer between the organism and the substrate by conduction, E_{evap} is energy loss or gain by evaporative cooling or condensation of water vapour, and E_{st} is energy temporarily stored by thermal gradients within the organism.

Colouration affects S_{abs}, which in turn affects behavioural thermoregulation. Of primary importance is the amount of solar infrared absorbed (as opposed to visual light), since this is the component of solar radiation which results in warming of the beetle's body. Dark coloured elytra may elevate body temperature by conduction of heat from the elytra to the thorax, or by convection, producing a warm air space under the elytra. Butterfly wings can serve both functions (Casey, 1981), and it is possible that *Cicindela* elytra do as well.

My work has show that, with respect to colouration, the relative extent of light elytral markings affects thermoregulatory time budgets in both *C. formosa* and *C. limbata.* Individuals with expanded light markings warm up less efficiently by basking, but do not overheat as readily during mid day. Colouration differences do not, however, seem to have any effect on diel or seasonal activity patterns. The colour patterns of adult *Cicindela* appear to serve a number of functions, including thermoregulation, substrate matching, mimicry, disruption by iridescence, aposematic colouration, and intraspecific signalling (Chapter III; Acorn, in press). I have argued that expanded light markings are a thermoregulatory adaptation for beetles in open, upland habitats where very high temperatures are commonplace. Most *Cicindela* in these habitats live on windblown sand or saline flats, and most of these beetles have expanded light markings (Chapter V; Willis, 1967). On light sand or saline soils, however, these colour patterns also enhance substrate matching, and thus the consequences of expanded markings may be both reduced predation and increased ability to remain active at high temperatures.

For the most part, it appears that tiger beetle thermoregulation consists of alternating periods of basking, stilting, and shuttling to shade. Basking beetles orient perpendicular to the sun's rays to maximize S_{abs} (Dreisig, 1980). By resting the body on the substrate, they also maximize T_{abs} and E_{cond} from the ground and E_{conv} from warm air near the ground; and minimize E_{conv} to cooler air above the ground, because of steep gradients of air movement and air temperature (Casey, 1981; Dreisig, 1980), and reradiated thermal energy (Norris, 1967) immediately above the substrate. Stilting, the functional opposite of basking, is a graded thermoregulatory mechanism which allows animals to proceed with other activities, such as feeding or mating, at high temperatures. Stilting is seen in tiger beetles, lizards (Norris, 1967), tenebrionid beetles, grasshoppers, and scorpions (Casey, 1981). Although animals cannot reduce T_{abs} by reflection (Burtt, 1981) lizards reduce incident thermal radiation by avoiding reflective substrates and small depressions, and by stilting, since a large proportion of incident thermal radiation comes from objects in close proximity to the organism (Norris, 1967). In arthropod studies, it has been argued that stilting serves to minimize E_{cond} (from the ground, and warmer air near the ground) and increase E_{conv} to faster moving air further out of the boundary layer (Casey, 1981). All three factors (T_{abs}, E_{cond}, and E_{conv}) are probably involved for all stilting organisms. Morgan (1985) has obtained empirical evidence that stilting reduces body temperature in *Cicindela tranquebarrica* Herbst. Another postural mechanism for reducing body temperature involves facing the sun, thus reducing the surface area available for warming (Morgan, 1985). Shuttling to a shaded spot, by definition, reduces S_{abs} for both beetles and their substrate, and thus T_{abs} is reduced, as is E_{cond} from the ground, and possibly E_{conv} from cooler air. In sunlight, body temperature warms toward an upper equilibrium temperature, and in shade it cools toward a lower equilibrium temperature. Between these two extremes are the temperature points at which beetles shuttle to shade or sunlight (Dreisig, 1985).

A number of other behavioural mechanisms for thermoregulation are also used by tiger beetles, primarily in conditions of extreme heat. Tiger beetles make use of cooler, moist substrates when dry ground is too hot (Guppy, et. al., 1983; Pearson and Lederhouse, 1987). On the Lake Athabasca sand dunes in northern Saskatchewan, Canada, I have observed aggregations of *C. hirticollis* Say and *C. limbata* on small patches of dark soil scattered throughout expanses of white sand. I did not measure temperature on either substrate, but the soil felt cooler to the touch than did the sand. At extremely high temperatures, flight may serve to quickly remove beetles from very warm microenvironments, in which thermoregulation is impossible. During the time budget experiments, in which beetles were unable to fly, those placed on overly warm substrates climbed grass stems, after repeated jumps which were presumably attempts at flight. Similar behaviour was observed in untreated *C. obsoleta* Say and *C. punctulata* Olivier, in Arizona (D. L. Pearson, in litt.). However, "during flight, all but the smallest insects produce heat sufficient to elevate thoracic temperature," (Casey, 1981), and the body temperatures of *Cicindela* caught at lights are higher than ambient air temperature (Pearson and Lederhouse, 1987). Nonetheless, the short flights of tiger beetles have been shown to result in convective cooling (Morgan, 1985), where heat loss to E_{conv} is presumably greater than heat production (M). Another response to prohibitive heat is to dig short burrows into the sand (Wallis, 1961). I have observed this in *C. limbata, C. lepida,* and *C. formosa,*; and it is also known for *C. hybrida* in Denmark (Dreisig, 1980), and *C. dongalensis* Klug in Kenya (Guppy, et. al., 1983).

Not all tiger beetles studied exhibit all of the above behaviours. Dreisig (1984) did not observe shuttling to shade in *C. hybrida*, Guppy et. al. (1983) did not observe stilting in *C. dongalensis*, and Morgan (1985) observed neither shuttling to shade nor burrowing at high temperatures in *C. tranquebarrica*. Whether all tiger beetles have the capacity to perform the above behaviours is unknown. However, the distribution of thermoregulatory mechanisms in a phylogenetic context could give numerous insights into the evolution of tiger beetles.

Although the role of colouration in modifying the behavioural thermoregulation of tiger beetles seems well established, one more counterargument deserves mention here. In some mammals and birds, dark coloured fur or feathers reduces S_{abs} by preventing incoming radiation from reaching the body surface, and insulating the warmed outer layer of fur or feathers from the skin (Walsberg, 1983). It is conceivable that dark elytra could serve a similar function, but this is not apparent in tiger beetles. A related argument is presented by Van Natto and Freitag (1986) who have proposed a functional analogy between tiger beetle bodies and thermos bottles, based on the assumption that iridescent colours of both the elytra and abdominal tergites reduce T_{abs} by reflection, while the sub-elytral airspace insulates against heat uptake through E_{conv} and E_{cond}. There are two problems with this idea. First, they present no convincing evidence that T_{abs} is reduced by reflectance. Second, they assume that "metallic" colours (actually multi-layered interference reflectors [Mossakowski, 1979]) will behave like real metals with respect to thermal properties, and thus reflect long wave infrared radiation. This argument is not in agreement with the current belief that "biological tissue, regardless of colour, absorbs all incident thermal [i.e. re-radiated long wave infrared] radiation" (Burtt, 1981).

Tiger beetle colouration can be examined with respect to its evolutionary and biogeographic origins as well as with respect to its thermoregulatory functions. Historically, much of the intraspecific colour variation in dune tiger beetles is likely to have arisen during the Holocene. Open sand habitats, other than major dune fields, appear and disappear quickly and frequently. Because of this, over relatively short spans of geologic time, colour variation within a species may alternate between broad geographic clines and discrete isolated populations. Even in the last hundred years, the pattern of colour variation has changed, possibly because of the Dust Bowl, road construction, and changes in cattle grazing.

The thermoregulatory characteristics of species can be used to construct an hypothetical explanation for observed patterns of food, time, and space use by the Empress tiger beetles. With respect to habitat use, the species with expanded light markings (*C. limbata* and *C. lepida*) are found on open sand habitats while those with less expanded or no light markings are found in dune margin habitats. This is an expected result of the thermoregulatory consequences of elytral pattern. Populations isolated in large dune fields undergo evolution of expanded light markings, and populations thus modified can and do inhabit more open ground. On the other hand, *Cicindela s. scutellaris* is found in the scurf pea zone, where it is may be better able to thermoregulate, in sympatry with its mimetic model, *Lytta nuttalli*. *Cicindela f. formosa* and *C. lengi* live in more vegetated areas, in accordance with the prediction that frequent access to shade is important for thermoregulation in darker beetles. I found no evidence for seasonal segregation of adults, an expected result of interspecific competition. Predation may have an effect, however, in that late summer emergence in *C. limbata* may act to minimize predation by *C. formosa*. With respect to food, Pearson and Mury's (1979) hypothesis that resource partitioning would result in character divergence with respect to mandible size is refuted by the essentially identical mandible sizes of *C. limbata* and *C. lepida*. It is still possible that diel segregation occurs between these species, but this possibility is not sufficient to uphold the hypothesis that interspecific competition is the primary structuring factor influencing coexistence among these five species.

Increasingly, the study of tiger beetle biology has come to focus on the importance of thermoregulation in open, sunlit habitats. My own work has served to connect this growing body of knowledge and theory with another large component of tiger beetle studies, namely the description of geographic colour variation. By placing colour variation in the context of its adaptive significance and historical development, I hope that I have in some ways validated the efforts of taxonomists concerned with intraspecific variation. However, although the importance of thermoregulation appears to be gaining general acceptance, I hope that I have also brought to focus the importance of such phenomena as mimicry, interspecific predation, and human disturbance of habitats for the understanding of tiger beetles. With so many people interested in this group of animals, for such a variety of reasons, it has been all too easy to develop a conventional wisdom. It remains, now that we have such a body of explanation, for creative and careful researchers to probe more deeply for the factors which have produced the amazing diversity of the genus *Cicindela*. Diverse taxa are perennially fascinating, and *Cicindela* is one such taxon; a group of beetles which, although instantly recognizable anywhere on earth, have been molded by the confluences of nature into a myriad of subtly different biological patterns.

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APPENDIX 1:

Plant species used in cluster analysis of pitfall trap sites. Names follow Moss (1983).

Agropyron (one or more species, not determined).
Artemisia frigida Willd.
Artemisia campestris L.
Calamovilfa longifolia (Hook.) Scribn.
Coryphantha vivipara (Nutt.) Britt. & Rose
Helianthus couplandii Boivin
Heterotheca villosa (Pursh) Shinners
Juniperus horizontalis Moench
Koeleria macracantha (Ledeb.) J. A. Schultes f.
Lygodesmia juncea (Pursh) D. Don
Oryzopsis hymenoides (R. & S.) Ricker
Psoralea lancoelata Pursh
Rosa woodsii Lindl.
Stipa comata Trin. and Rupr.